DIFFERENTIAL HABITAT USE BY A LOCAL POPULATION OF THE VELVET-FURRED RAT, RATTUS LUTREOLUS VELUTINUS (THOMAS 1882), IN WET SCLEROPHYLL FOREST, SE TASMANIA.

BY

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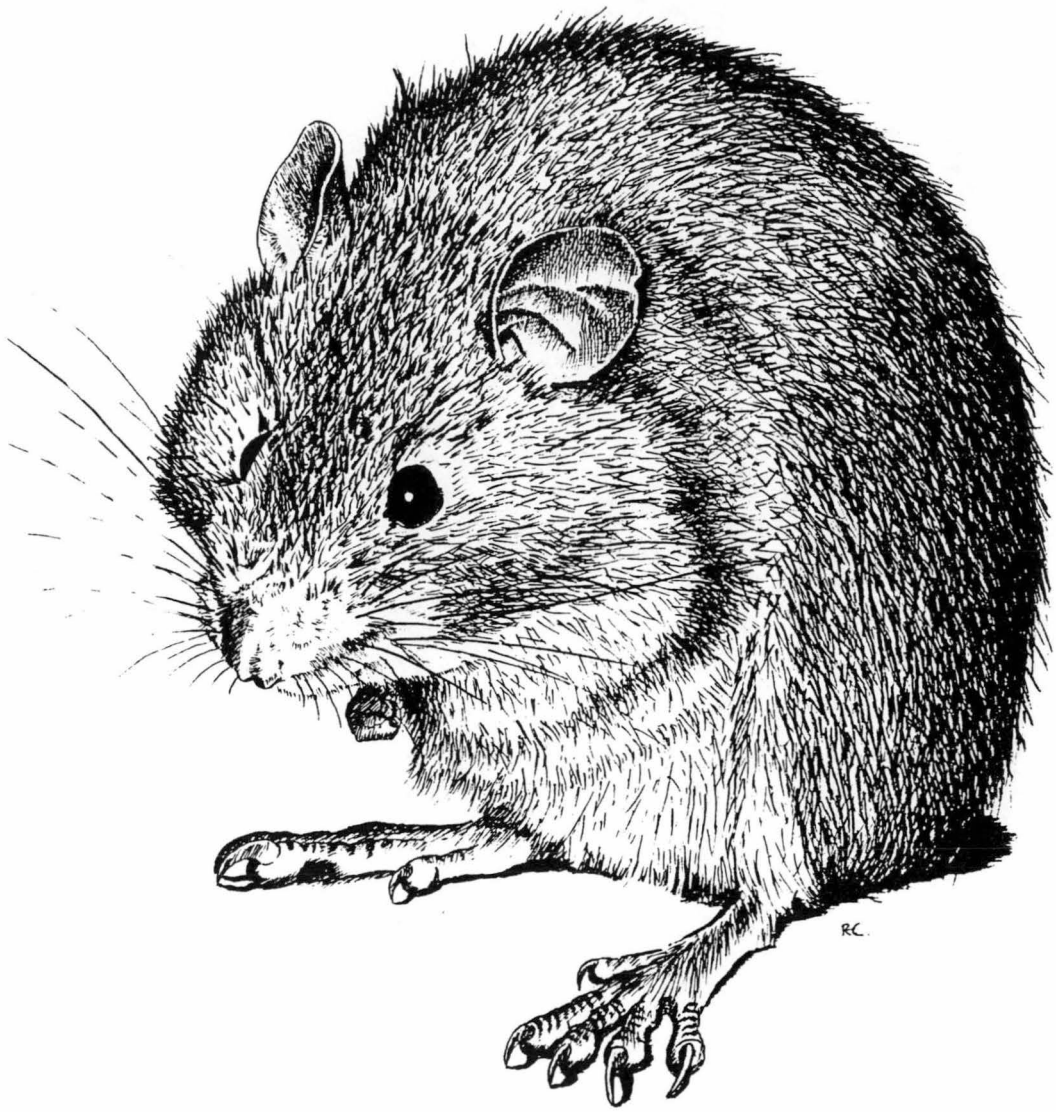
A thesis submitted in fulfilment of the requirements
for the degree of
Master of Science
University of Tasmania
January, 1991.

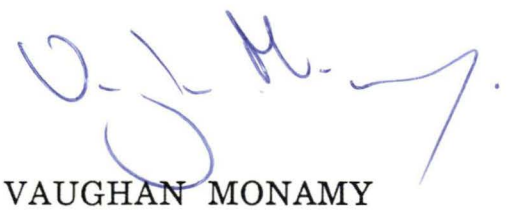


...I'm truly sorry man's dominion
Hath broken Nature's social union,
And justifies that ill opinion
Which makes thee startle
At me, thy poor earth-born companion,
And fellow mortal.

Robert Burns "An Address to a Mouse."

DECLARATION

This thesis represents my own work and contains no material which has been accepted for the award of any other higher degree in any tertiary institution. To the best of my knowledge and belief this thesis contains no material previously published or written by another person, except where due reference is made in the text.



VAUGHAN MONAMY

ABSTRACT

This study investigates a reported decline in the proportion of male *Rattus lutreolus velutinus* in a trappable population during winter. A four hectare trapping grid was maintained between March 1989 and June 1990 in wet sclerophyll forest which had been burned by wildfire in 1967. The forest community displayed both structural and floristic heterogeneity. Four habitat groups were defined and capture data from 17 four-weekly trapping sessions are compared within these groups. *R. l. velutinus* exhibit a clear preference for areas of densest cover to one metre height and an avoidance of areas with little or no ground cover. During winter, areas of densest cover are utilized almost exclusively by females; males occupy areas with less cover at lower densities. During the breeding season, females continue to be captured in areas of densest ground cover. These areas are visited by numerous males in reproductive condition.

An ecophysiological assessment of individuals in the trappable population was undertaken using routine blood sampling and the influence of environmental and artificial stressors on some haematological and endocrinological parameters is examined. Significant differences are evident between sexes for some measured parameters but no important differences are evident between the physiological states of individuals captured in different habitat groups.

The results of this study indicate that a local population of *R. l. velutinus* may use habitat differentially but that individuals captured in different habitat groups do not differ in their physiological profiles or their ability to cope with environmental stressors. The intersexual difference in habitat use is discussed in relation to social spacing, resource utilization and female choice.

ACKNOWLEDGEMENTS

Scientific studies are rarely, if ever, completed without the able and willing assistance of many people. This project is no exception and it is a pleasure to thank the following people for the enthusiastic support they offered.

Permission to conduct the study in the Mt. Wellington Flora and Fauna Reserve was given by the Tasmanian Department of Parks, Wildlife and Heritage and the Hobart City Council. I thank the University of Tasmania and the trustees of the M. A. Ingram Trust (Victoria) for generous financial support.

I am grateful to Professor Michael Stoddart for his excellent supervision in all aspects of the project. I thank Dr. Sue Jones and Dr. Adrian Bradley who both gave willingly of their time, particularly when steroid assays ought to have been completed yesterday.

A special thank you to Dr. Sally Bryant who pushed when it was needed the most.

Stephen Mallick and Sam Thalman agreed to the almost impossible when setting up the trapping grid - 20 metres is often a long way. Many people cheerfully spent a day or two (never three) assisting with the early morning clearing of traps: Mirranie Barker, Sally Bryant, Rick Crossland, Georgina Davis, Murray Hassler, Jean Jackson, Menna Jones, Mary Mulcahy, Sarah Munks, Sue Parsons and Sam Thalman. Thank you all.

I thank Kristen Williams and especially Mirranie Barker for assistance in the collection of vegetation data, Rod Fensham for advice on the use of 'ECOPAK' and Gintaris Kantvilas and Dennis Morris of the Tasmanian Herbarium for instant plant identification.

Phil Barker and Bob Mesibov kindly read an early draft of the thesis and Rick Crossland generously provided the ink drawing for the frontispiece.

Technical assistance was always available at a moment's notice and for this I am grateful to Kate Hamilton, Richard Holmes and Wayne Kelly. Sherrin Bowden was always on hand when typing was needed, Barry Rumbold ensured that there was always enough money in someone's research grant for me to spend and Ron Mawbey generously showed me how to recognize the wildlife of Tasmania and a table tennis topspin forehand.

I thank Professor John Eisenberg and Dr. Robert Rose for stimulating discussions while they were visiting the department, Marg Morrice and Kristen Hynes for putting up with the interruptions and Wendy Davidson and Alan Macfadyen for improving my grammar.

Very special thanks go to my partner, Mirranie Barker who provided the emotional and financial support that made the goal achievable and to Wingnut for not complaining when I was too tired to take her for a walk.

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CHAPTER ONE
INTRODUCTION

1.1 Introduction

This study aims to clarify observations made by Stoddart and Challis (1991) during the collection of field data on the habitat preferences of the long-tailed mouse, *Pseudomys higginsi* (Trouessart). A 0.5ha trapping grid was maintained by these authors in wet sclerophyll forest on the SE slopes of Mt. Wellington, Tasmania from September 1986 until April 1988. Data were obtained from this grid on *P. higginsi* and the sympatric native murid *Rattus lutreolus velutinus* (Thomas). During the 1987 winter, a marked decline in the proportion of male *R. l. velutinus* in the trappable population was recorded (Stoddart and Challis, pers. comm.). Only two sub-adult males were captured on eight occasions during six trapping sessions between 1 April and 28 August 1987 (four nights per session; 49 traps; 1,176 trap nights). At the same time, seven adult and five sub-adult females were caught 88 and 28 times, respectively (see Table 1.1).

Several questions arose from this observation. Was the low capture rate for males due to a sex bias in trappability? Such a disparity in trap-revealed sex ratio had not been reported previously for *R. l. velutinus* although trapping programs involving the capture of this species had been undertaken in similar forest habitat (Hocking 1975; Murray 1980). Alternatively, do male and female *R. l. velutinus* have differing resource requirements and are therefore likely to be caught in different habitat types at different times? Differential resource use by the two sexes of a species is common in some birds (Robins 1971; Anderson and Shugart 1974; Hogstad 1976) and reptiles (Schoener 1967, 1968) but intersexual differences in the use of habitat by small mammals has only been demonstrated infrequently (Stoddart and Braithwaite 1979; Bowers and Smith 1979; Morris 1984; Seagle 1985; Belk *et al.* 1988).

To date, studies of habitat utilization by *R. l. velutinus* have shown a requirement for green vegetation and dense ground cover (Hocking 1975; Murray 1980; Norton 1983; Driessen 1987). This is supported by research on the mainland Australian sub-species *R. l. lacus* (Taylor 1975) and *R. l.*

Table 1.1: Summary of captures of *Rattus lutreolus velutinus* from a 0.5ha trapping grid, Mt. Wellington, Tasmania between September 1986 and April 1988. Numbers in parentheses denote total captures. (Unpublished data provided by D.M. Stoddart and G. Challis.)

SEASON	MALES	FEMALES
BREEDING SEASON ('86/ '87) (9 TRAPPING SESSIONS)	19 ADULTS (116)	9 ADULTS (118)
WINTER (1987) (6 TRAPPING SESSIONS)	0 ADULTS 2 YOUNG (8)	7 ADULTS (88) 5 YOUNG (28)
BREEDING SEASON ('87/ '88) (9 TRAPPING SESSIONS)	13 ADULTS (66)	13 ADULTS (129)

lutreolus (Braithwaite 1979, 1980, 1982; Braithwaite and Gullan 1978; Braithwaite and Lee 1979; Watts and Braithwaite 1978; Lunney 1980). No examination of intersexual difference in resource use by *R. lutreolus* has been published.

Another possibility is that each sex has similar requirements but intersexual competition limits the availability of common resources or habitat for either sex. Such a strategy has been demonstrated for the brown bandicoot, *Isoodon obesulus* (Shaw) in regenerating heath habitat (Stoddart and Braithwaite 1979). *I. obesulus* shows strong sexual dimorphism with adult males 30% larger than adult females. Stoddart and Braithwaite (1979) showed that adult males occupy a preferred habitat type and were intolerant of other males and females. Because of their pugnacious behaviour, males occupied this habitat type to the exclusion of adult females.

No sexual dimorphism has been reported for *R. l. velutinus* although captive studies have shown that females may be intolerant of males in the non-breeding season (Morris 1969; Mallick 1989).

This investigation tested whether the reported decline in the proportion of males in the trappable population was a real biological phenomenon or an artefact of trapping.

1.2 Aims

1.2.1 Confirmation of the reported decline

The initial aim was to confirm the decline recorded by Stoddart and Challis (pers. comm.) using live-trapping. Their trapping grid was relatively small (0.5ha) and only a small number of animals had been caught. A larger trapping grid was planned for this study in the expectation of an increased capture rate. An enlarged trapping grid which included the original grid was not possible due to the proximity of the original to walking trails and roads. Instead, an area was surveyed approximately 500m NE where a much larger grid could be maintained (see Figure 1.1).

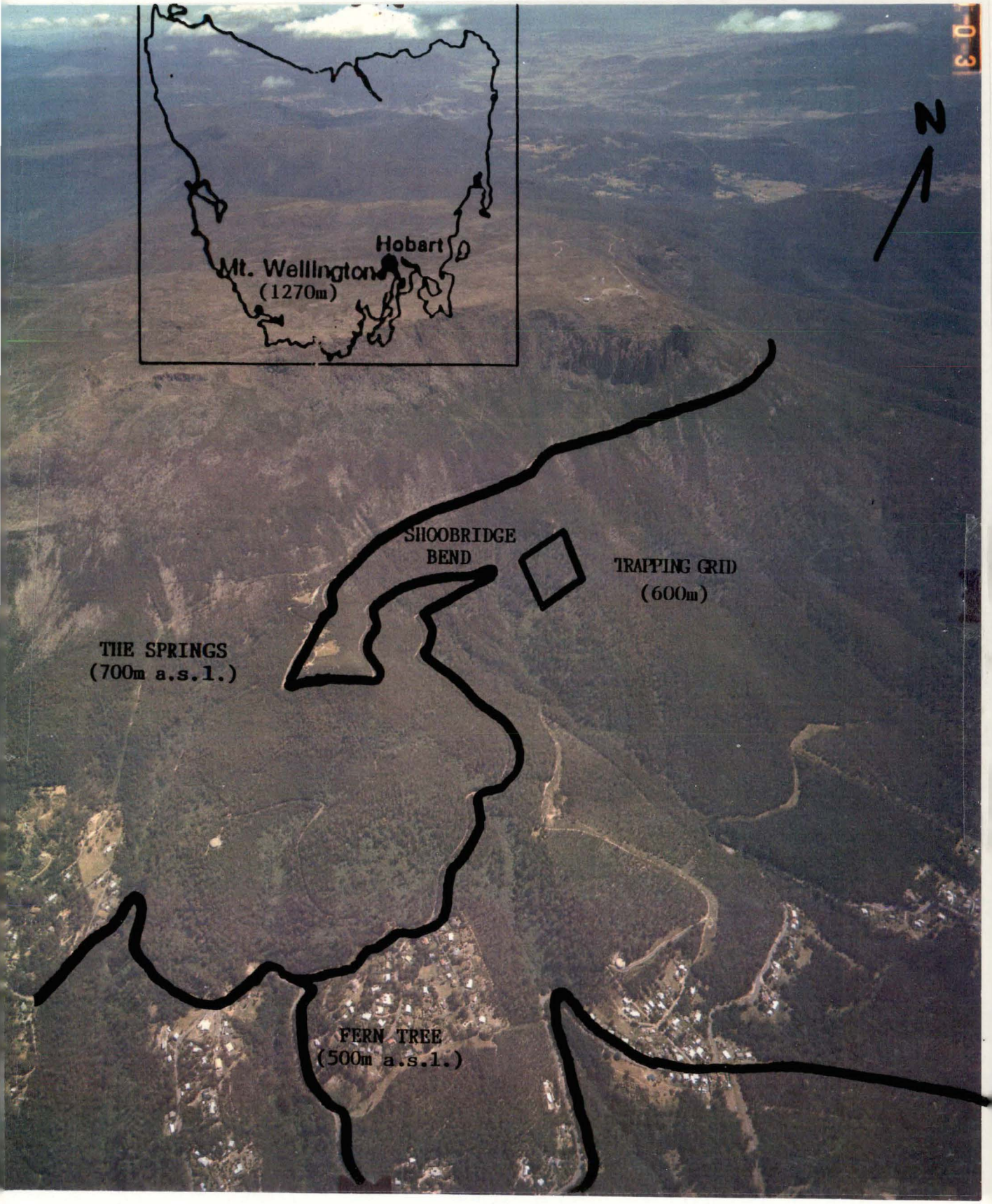


Figure 1.1: Mt. Wellington, Tasmania (1 270m). The trapping grid is shown NE of Shoobridge Bend.

Figure 1.1: Mt. Wellington, Tasmania (1 270m). The trapping grid is shown NE of Shoobridge Bend.

1.2.2 Bias in trappability

To test for biases in trappability, a trapping program was conducted that involved the routine sampling of a population of *R. l. velutinus* throughout the year. This allowed analyses by sex and season of the capture data.

Additionally, the possible effects of residual trap odour on the subsequent capture of individuals were tested. Many rodent species have social systems characterized by relatively large ranges with some degree of overlap (Stoddart 1974). Olfaction may aid in the maintenance of spatial organization (Mykytowycz 1974) as well as providing a means of communicating information about such factors as individual range, sex or receptivity between widely spaced conspecifics.

Residual odours from previous occupants of live traps have been shown to influence subsequent trap entries in some small mammal species (Boonstra and Krebs 1976; Stoddart 1982; Stoddart and Smith 1984). *R. l. velutinus* leads a semi-solitary life and may use olfactory communication to some extent (Mallick 1989). If this is the case, and residual odours contain biological information that maintains social spacing, then the deposition of such odours in traps could conceivably lead to a bias in trapping if individuals either avoid or are attracted to such odours (see Section 2.6.4).

1.2.3 Differential habitat use

The original grid had been situated in an area of vegetation with no discernible variation in floristic or structural attributes. To determine whether individual *R. l. velutinus* were using habitat differentially, an area needed to be located which included a similar habitat type to that extending throughout the grid of Stoddart and Challis (1991), but which also included areas that were both structurally and floristically distinct.

1.2.4 Ecophysiology

Are individuals in particular habitat types more or less able to cope with the rigours of daily existence depending on the resources available to them? To answer this question, routine blood sampling was carried out as a means of monitoring physical well-being through a variety of haematological

indices. Additionally, plasma corticosterone assays were conducted to assess changes in seasonal stress levels; evidence of wounding was recorded and obvious ectoparasitic burdens noted. In this way, physiological and endocrine parameters could be correlated with behavioural changes through the year (see Chapter 5).

1.3 The study area

1.3.1 Introduction

A four hectare trapping grid was surveyed near Shoobridge Bend in the Mt. Wellington Flora and Fauna Reserve, Tasmania (42° 56' S; 147° 15' E). Located at altitudes between 550m and 620m a.s.l. on the SE slopes of Mt. Wellington (1,270m), the grid included areas burned by wildfire in February 1967.

A qualitative survey of the vegetation was undertaken prior to preliminary trapping. Structural and floristic heterogeneity was apparent in the vegetation, as well as variation in slope and aspect (see Section 1.3.4). Results of a quantitative survey of the vegetation are presented in Chapter 3.

1.3.2 Geological features

Mount Wellington forms the eastern end of the Mt. Wellington Plateau and acts as a watershed between the lower reaches of the Huon and Derwent Rivers.

The study area is located on podsols over quaternary dolerite talus. The podsols consist of loams containing large amounts of organic matter which overlie grey and yellow clays. In areas where drainage is restricted, accumulation of organic matter has resulted in a peaty sand that directly overlies the clay sub-soil (Martin 1939). The dolerite talus weathers to a rocky soil holding little surface water. Ground and surface water from higher altitudes flows readily through and underneath the talus, only reappearing as small streams in outcrops of the underlying sandstones and mudstones. Such an outflow appears within the study area. One side of the trapping grid lies on a scree slope of large dolerite boulders.

1.3.3 Climate

Climatic data were obtained from the Bureau of Meteorology, Hobart. Mt. Wellington has a temperate maritime climate. Average annual temperatures range between 4.4°C (minimum) and 11.0°C (maximum). No direct temperature or rainfall data are available for the study area but annual rainfall data are available for Fern Tree (500m a.s.l.: 1967-1989 : 1,164mm); and The Springs (700m a.s.l.: 1921-1985 : 1,374mm: see Figure 1.1). By interpolation, mean annual rainfall at the study site is estimated to be approximately 1,270mm. Snow may be recorded in any month.

1.3.4 Vegetation

Wet sclerophyll forest communities are typically two-layered with a eucalypt overstorey and a mesophytic understorey. In Tasmania, the most common eucalypts found in lowland areas are *Eucalyptus obliqua* and *E. delegatensis* (Duncan and Brown 1985). *E. regnans* forms a monotypic canopy stand in wetter gullies. The eucalypts shade a sub-canopy which includes the small trees *Bedfordia salicina, Pomaderris apetala, Olearia argophylla, Pittosporum bicolor* and *Prostanthera lasianthos.* Floristics, sub-canopy density and height vary considerably with the availability of water, but generally the sub-canopy has a projective cover of approximately 90% (Jackson 1981). Ferns are common with *Polystichum proliferum, Dicksonia antarctica* and *Blechnum wattsii* predominating. Rainforest species such as *Atherosperma moschatum* and *Nothofagus cunninghamii* sometimes occur in the understorey.

Floristic aspects of the vegetation at Shoobridge Bend have been described by Ratkowsky and Ratkowsky (1977) and Corbett (1981). The overstorey is typical of a wet sclerophyll formation (*sensu* Jackson 1981) comprising mainly *E. delegatensis,* with wetter areas shaded by *E. regnans.* A dense sub-canopy is dominated by regenerating broad-leafed species (*B. salicina, P. apetala* and *O. argophylla*) occurring at heights from two to eight metres. A ground cover consisting mainly of ferns (*B. wattsii, P. proliferum* and *D. antarctica*) occurs throughout the wetter areas. Numerous dead trees or stags and large decaying logs - remnants of

the very severe 1967 wildfire - are also a major feature of the habitat.

A qualitative survey of the study area revealed several structurally and floristically distinct vegetation types. These included: areas of dense fern understorey shaded by a mature *E. regnans* overstorey; an area of exposed dolerite scree with ferns and grasses growing between large boulders and shaded by mature *E. delegatensis*; and a region of dense regenerating *B. salicina* and *P. apetala* with sparse ground cover.

The survey showed that wet sclerophyll communities are not floristically or structurally uniform. They are influenced by various habitat conditions; random environmental and population processes; and interactions between plant species. Such processes illustrate the dynamic nature of such communities and may influence the way in which small mammals utilize habitat resources.

CHAPTER TWO
THE STUDY POPULATION

2.1 Introduction

Having located an area of vegetation that offered structural and floristic heterogeneity, a trapping program to investigate possible differential use of habitat by a local population of *R. l. velutinus* was conducted. To satisfy the study aims, the program had to permit the trapping of a sufficient number of individuals to allow observations to be made about population structure, habitat use and social spacing. In this chapter, data collected during the study are presented.

2.2 Sampling Methods

A square trapping grid of 100 trap points was surveyed using a compass and measuring tape. Wire markers were located 20m apart along both axes of the grid and a folding aluminium live trap (33x10x10cm: Elliott Scientific Equipment, Upway, Victoria) was placed within a two metre radius of each marker. The 20m spacings gave an overall sampling area of 4ha.

Traps were baited with a mixture of peanut butter and rolled oats. Plastic bags were placed over traps to provide shelter and shredded paper was used as nesting material. Only one trap death was recorded for *R. l. velutinus* in 6 800 trap nights and 706 captures.

Two preliminary trapping sessions were undertaken in March and April 1989 to determine whether the trapping grid had been located in sufficiently well-populated habitat. A further 15 investigative trapping sessions were then conducted at four-weekly intervals between May 1989 and June 1990. Each trapping session consisted of four consecutive trapping nights. Traps were emptied and reset starting at first light each morning. Soiled bedding was replaced after each capture or as required. Traps were removed from the grid and cleaned after each session.

At first capture, individuals were ear-tagged with a numbered fingerling fish tag (Size FF: Salt Lake Stamp Company, Utah, U.S.A.). Ear-tagging was preferred to toe-clipping as a means of identification as it was

considered more humane (*ad hoc* Committee on Acceptable Field Methods in Mammalogy 1987). No tags were lost during the study.

At the first capture in each trapping session, a blood sample not exceeding 500µl, or 5% of total blood volume was collected for analysis (see Section 5.2.1).

At every capture, the weight, reproductive condition and grid position of each recaptured individual were recorded. Weights were measured to ±1g using a Salter® 200g spring balance. Additionally, teat size and colour were recorded for adult females. Lactating females had enlarged (≈2mm long) teats; post-lactating females had black, flattened teats. In males, testes were noted as being in a scrotum, in the abdomen or intermediate between the two. Abdominal denotes the condition in sub-adult and overwintering adult males where the testes are small and retained inguinally. At the onset of breeding, the testes enlarge and descend into a large scrotum. These observations were used to determine 'seasons' in the life history of *R. l. velutinus* (Table 2.1).

Animal abundance was estimated using direct enumeration (minimum numbers known to be alive, MNA: see discussion in Section 2.6.2). Evidence of wounding (tail-scarring) and obvious burdens of ectoparasites were also noted. All animals were released at the point of capture.

2.3 Trapping program

2.3.1 Preliminary trapping

Preliminary trapping was undertaken from 20 - 24 March 1989 and from 3 - 7 April 1989.

Capture results are shown as the first two trap sessions in Table 2.2. The first session resulted in 52 captures of 26 individual *R. l. velutinus*. In the second session, 21 individuals, 17 of which had been captured and tagged previously, were caught 46 times.

Table 2.3 shows the number of individuals captured in each sex and age class. Animals were classed as either adult, sub-adult (i.e., born in the first litter of the year) or juvenile (i.e., born in the second litter of the year) based on weight and reproductive status. Adults were still in breeding condition in

Table 2.1: Characteristics used to classify seasons in the life history of *R.l. velutinus*.

SEASON	CHARACTERISTICS
Dispersal	Adults in breeding condition
20.iii.89	Unmarked young of the year entering the trappable
- 5.v.89	population
Winter	Adults no longer in breeding condition
4.ix.89	Regular trapping of resident animals
- 16.x.89	
Breeding	All animals in breeding condition
13.xi.89	Influx of previously unmarked individuals
- 9.iii.90	
Dispersal	
2.iv.90	No animals in breeding condition
- 1.vi.90	Influx of unmarked young of the year

Table 2.2: Summary of individual captures of *R. l. velutinus* for each trapping session. Number of captures in parentheses.

TRAP SESSION	DATE	MALES	FEMALES
	Dispersal		
Preliminary			
1	20.iii.89	13 (21)	13 (31)
2	3.iv.89	11 (22)	10 (24)
Investigative			
3	1.v.89	9 (21)	7 (16)
	Winter		
4	29.v.89	5 (16)	7 (18)
5	26.vi.89	4 (11)	9 (24)
6	24.vii.89	5 (14)	9 (30)
7	21.viii.89	4 (15)	9 (27)
8	18.ix.89	4 (13)	9 (29)
9	16.x.89	6 (20)	10 (30)
	Breeding		
10	13.xi.89	14 (33)	9 (20)
11	11.xii.89	14 (39)	8 (19)
12	8.i.90	9 (18)	5 (13)
13	5.ii.90	9 (21)	7 (16)
14	5.iii.90	5 (17)	8 (17)
15	2.iv.90	5 (11)	4 (9)
	Dispersal		
16	30.iv.90	9 (21)	11 (25)
17	28.v.90	10 (23)	9 (22)
	Total captures	42 (336)	31 (370)

early autumn 1989 and weighed >100g. Sub-adults showed no evidence of reproductive maturity (i.e., teats not enlarged; testes abdominal) and weighed 70-90g. Juveniles weighed 45-60g. No individual captured at this time weighed less than 45g.

The results of the preliminary trapping program showed that the study area contained a trappable population with sufficient adult and young individuals to allow conclusions about seasonal changes in sex ratio and habitat use to be made.

2.3.2 Investigative trapping

Investigative trapping commenced on 1 May 1989 and continued until 1 June 1990 (Table 2.2). During the 15 sessions, 231 traps (3.85%) were sprung without capturing an animal. These occurrences, known as trap attacks, were not recorded during preliminary trapping. Such events were usually associated with trap disturbance and damage, probably caused by brushtailed possums, *Trichosurus vulpecula* (Kerr). The most common sign of disturbance was trap doors being pulled outwards. Occasionally branches were forced through both entrances, effectively holding both doors down. One trap was retrieved from a tree branch over two metres above the ground. There was no obvious seasonal pattern of trap attacks on the grid with a mean of 15.4±11.9 (1 S.D.) attack events recorded per session.

Human interference with traps was noted on 4 December 1989. Traps were displaced and four were stolen. (The latter were found on the 'Circle' walking track within the Mt. Wellington Flora and Fauna Reserve two days later.) A sign describing the research program was placed at the beginning of the grid. There were no subsequent incidents of disturbance during the study.

2.3.3 Numbers of individuals caught

1,208 small mammal captures were recorded throughout the preliminary and investigative sessions, an overall trapping success of 17.6% (range: 9.8-23.5% per session). 73 individual *R. l. velutinus* were trapped a total of 706 times and represent 58.4% of all small mammal captures. A summary of vertebrate captures is presented in Table 2.4. For the 15

Table 2.3: Number of individuals in three age classes captured during preliminary trapping (March-April 1989). Total number of captures in parentheses; see text for explanation of age classes.

AGE CLASS	MALES	FEMALES
ADULT	6 (25)	3 (12)
SUB-ADULT	4 (16)	9 (28)
JUVENILE	4 (11)	4 (6)

Table 2.4: Summary of vertebrate captures recorded throughout the study.

SPECIES	CAPTURES	(%)
Small mammals:		
Rattus lutreolus velutinus	706	58.4
Antechinus swainsonii	257	21.3
Pseudomys higginsi	212	17.5
Rattus norvegicus	18	1.5
Mus musculus	15	1.3
TOTAL	**1208**	**100**
Birds:		
Superb Blue Wren, *Malurus cyaneus*	4	
Olive Whistler, *Pachycephala olivacea*	1	
Grey Butcherbird, *Cracticus torquatus*	1	

investigative trapping sessions, only two age classes were used, 'adult' or 'young of the year'. Individuals recorded as juvenile or sub-adult in the preliminary sessions (Section 2.3.1) were grouped as young of the year.

Table 2.5 presents a calendar of captures during the study. Estimates of MNA for each session are shown in Figure 2.1.

The mean number of females in the trappable population was 8.1±1.8 (1 SD) per session. The lowest capture rate of females was in April 1990 (4 individuals); the highest was in May 1990 (11 individuals). This period coincided with a time late in the breeding season prior to and immediately after the entry of juveniles of both sexes into the trappable population (April and May respectively: see Section 2.7).

The number of males in the trappable population was more variable (7.5±3.4: 1 SD). Lowest capture rates were recorded in winter (4 individuals caught in June, August and September). The highest capture rate coincided with the onset of breeding with 14 individuals caught in November and again in December 1989.

The average MNA for females for any trapping session was 9.5±1.8 (1 SD). The mean MNA for males was 8.0±3.3 (1 SD).

2.4 Growth and reproduction

2.4.1 Body weights

The mean weight at which young of the year entered the trappable population was 52±10g (1 SD: n=12). The lowest weight at which a young of the year entered the trappable population was 35g in February 1990. The highest weight recorded in the study was 144g for an adult male in December 1989.

Mean body weights for three age classes are shown in Figure 2.2. A marked increase in male body weight prior to the onset of breeding was evident. This adult weight was then maintained throughout the reproductive period. Mean sub-adult female weights remained at a lower level until September 1989, then rose quickly through October and November 1989 before stabilizing at a weight equivalent to that of adult males.

Table 2.5a: Calendar of captures for female *R. l. velutinus* (Number in bold type denotes first capture; asterisk denotes individual not captured but known to be alive because of subsequent capture(s)).

1989	Mar	Apr	May	Jun	Jun	Jul	Aug	Sep	Oct	Nov	Dec	1990	Jan	Feb	Mar	Apr	May	Jun
Trapping Session	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**		**12**	**13**	**14**	**15**	**16**	**17**
Born <1989																		
	10	10	10	10	10	10	10	10	10	10	10		-	-	-	-	-	-
	15	15	-	-	-	-	-	-	-	-	-		-	-	-	-	-	
	17	17	17	17	17	17	17	17	17	17	17		17	17	17	-	-	-
	27	27	*	*	27	27	27	-	-	-	-		-	-	-	-	-	-
		42	*	*	*	*	*	*	*	*	*		42	42	42	*	42	-
	89	89	89	89	89	89	89	89	89	-	-		-	-	-	-	-	-
Young of Year 1989																		
	1	1	1	1	1	1	1	1	1	1	1		1	1	*	*	1	-
	9	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-
	12	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-
	18	18	18	18	18	18	18	18	18	18	18		18	18	18	-	-	-
	23	23	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-
	28	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-
	29	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-
	-	-	-	-	**51**	51	51	51	51	51	51		-	-	-	-	-	-
	-	-	**52**	*	*	*	*	*	52	52	-		-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	**53**	53		-	-	-	-	-	-
	-	-	-	-	-	-	-	**55**	55	*	*		*	55	55	55	55	55
	-	-	-	**67**	67	67	67	67	67	67	-		-	-	-	-	-	-
	69	69	69	69	69	69	69	69	69	69	69		69	69	69	69	69	69
	-	-	-	-	-	-	-	-	-	-	**88**		-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	**210**	210
Young of Year 1990																		
	-	-	-	-	-	-	-	-	-	-	-		-	**82**	82	-	-	-
	-	-	-	-	-	-	-	-	-	-	-		-	-	**200**	200	200	200
	-	-	-	-	-	-	-	-	-	-	-		-	-	**201**	201	201	201
	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	**206**	-
	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	**213**
	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	**220**
	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	**221**	-
	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	**222**	222
	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	**223**
	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	**224**	-
Estimated MNA	**13**	**10**	**9**	**10**	**11**	**11**	**11**	**11**	**11**	**11**	**10**		**6**	**7**	**9**	**6**	**11**	**9**

Table 2.5b: Calendar of captures for male *R. l. velutinus* (Number in bold type denotes first capture; asterisk denotes individual not captured but known to be alive because of subsequent capture(s)).

	1989 Mar	Apr	May	Jun	Jun	Jul	Aug	Sep	Oct	Nov	Dec	1990 Jan	Feb	Mar	Apr	May	Jun
Trapping Session	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Born <1989																	
	11	11	11	11	11	11	11	11	11	11	11	11	-	-	-	-	-
	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	33	33	33	-	-	-	-	-	-	-	-	-	-	-	-	-	
Young of Year 1989																	
	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	5	5	5	5	5	5	5	5	5	5	5	-	-	-	-	-	-
	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	14	14	14	14	14	14	14	14	14	14	14	14	14	-	-	-	-
	19	19	19	19	19	19	19	19	19	19	19	-	-	-	-	-	-
	20	20	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	22	*	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	24	24	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	26	26	*	*	*	26	*	*	26	26	26	26	26	26	*	26	26
	34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	**36**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	**37**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	**41**	41	41	41	41	-	-	-
	-	-	-	-	-	-	-	-	-	**44**	44	-	-	-	-	-	-
	-	**45**	45	45	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	**46**	46	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	**47**	47	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	**49**	49	49	49	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	**54**	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	**56**	56	56	56	-	-	-	-
											57	*	57	57	57	57	57
	-	-	-	-	-	-	-	-	-	**59**	59	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	**60**	-	60	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	61	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	64	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	**68**	-	-	-	-
	-	-	-	-	-	-	-	-	-	**80**	*	80	80	80	80	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	**90**	90	90	90	90
Young of Year 1990																	
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**202**	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**203**	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**204**	204	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**205**	205
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		**207**
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**209**	209
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**214**	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**217**
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**219**
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**225**	225
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**230**
Estimated MNA	**13**	**12**	**10**	**5**	**5**	**5**	**5**	**5**	**6**	**14**	**15**	**10**	**9**	**5**	**6**	**9**	**10**

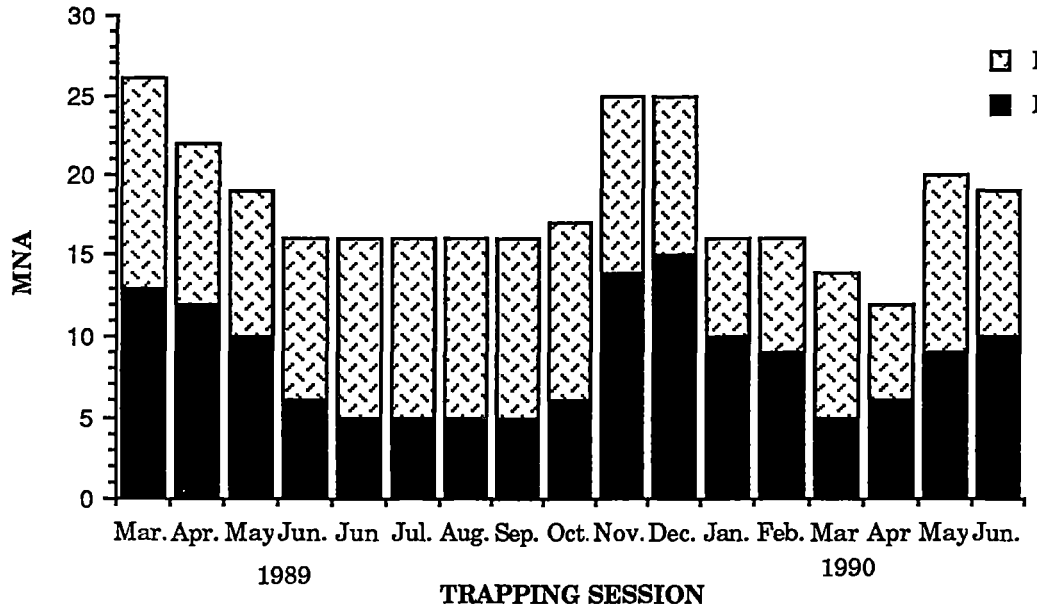


Figure 2.1: Minimum numbers known to be alive for each trapping session

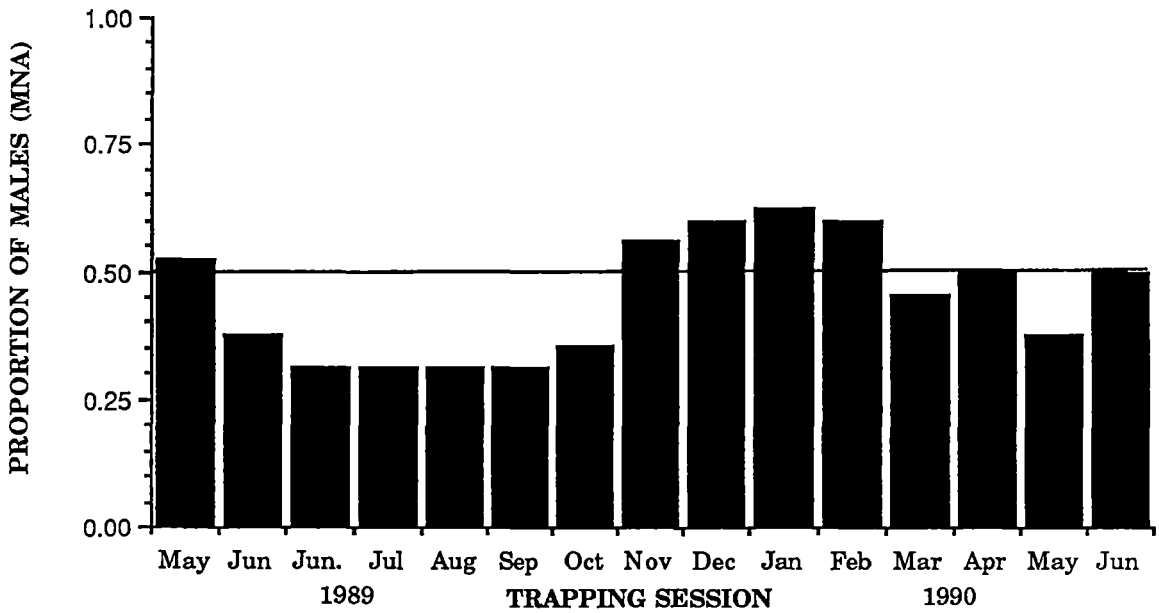
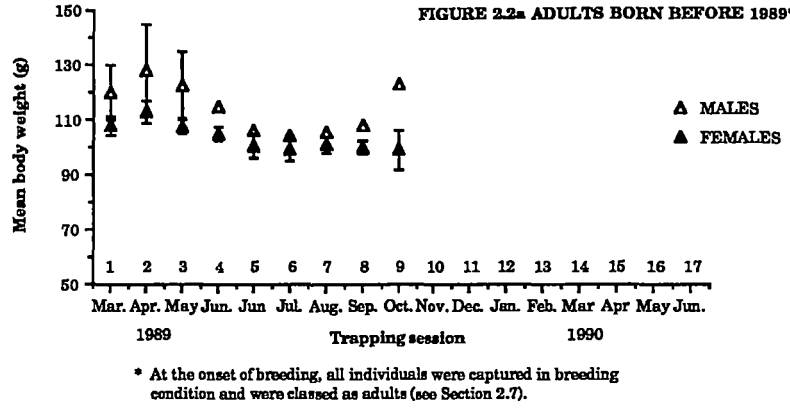
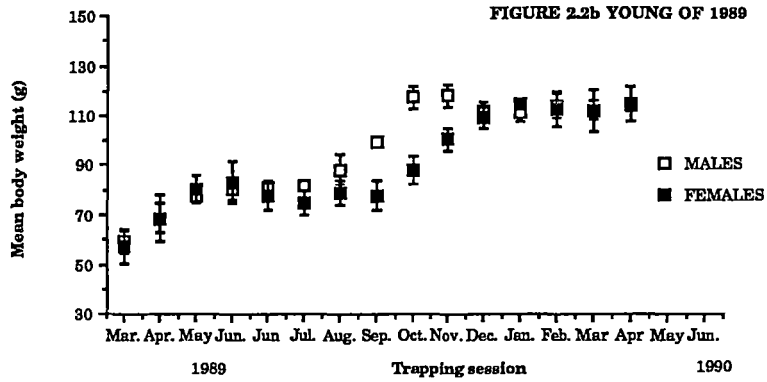


Figure 2.3: Sex ratios expressed as MNA for each trapping session. The horizontal line denotes parity.



* At the onset of breeding, all individuals were captured in breeding condition and were classed as adults (see Section 2.7).



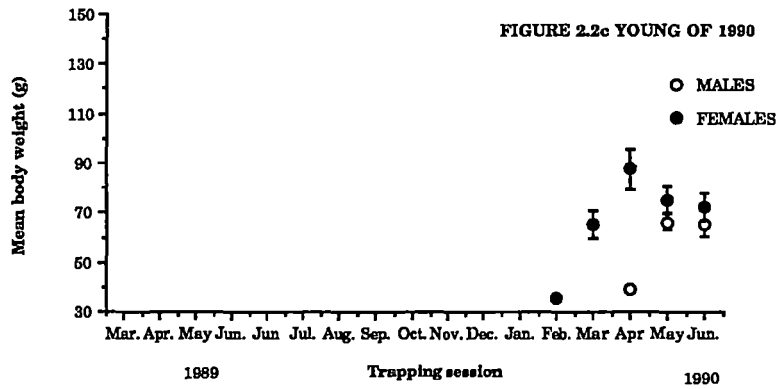


Figure 2.2: Body weights for three age classes (means ± 1 SD). (Trapping sessions 4 and 17 are both depicted as 'June'. Trapping actually commenced in the last days of May - see Table 2.2.)

2.4.2 Reproductive status

R. l. velutinus is a seasonal breeder. Breeding commences in October and up to two litters may be produced before the breeding season nears its end in March/ April (Green 1967; Taylor and Horner 1973). In this study, all evidence of reproductive activity was gone by June. That is, adult females had black, flattened teats indicating that lactation had ceased and the testes of adult males were abdominal. In October 1989, all males caught had scrotal testes. Lactating females were first recorded in December 1989 and the first young of 1990 was caught on 7 February. An influx of young of the year for 1990 was recorded in April and May 1990, the months during which they are dispersing and establishing ranges.

2.5 Sex Ratio

The sex ratio for the whole study was 42 males : 31 females. Sex ratios, expressed as the minimum proportion of males known to be alive in the trappable population, are shown in Figure 2.3. Eight of the 17 trapping sessions showed a female bias; seven a male bias; and two had equal numbers of males and females.

The decline in the number of males in the trappable population during winter observed by Stoddart and Challis was not recorded to the same extent in this study. Chi-square analyses of MNA estimates revealed no significant deviation from an even sex ratio during any trapping session (Table 2.6).

Seasonal changes in sex ratio were also tested for the breeding and winter seasons. The proportion of males known to be alive was lowest in winter but chi-square analysis of a 2 x 2 contingency table (Male-Female/ Winter-Breeding) revealed no significant deviation from the anticipated sex ratio of 1:1 (χ^2=1.7, d.f.=1, P>0.1).

The number of individuals in the trappable population during winter was low. Only four males and nine females were recorded as residents at this time (Section 2.6.3). Nevertheless, these data are sufficient to indicate that a null hypothesis of equal sex ratio should not be rejected. A discussion of the implications of these data is given in Section 2.8.

Table 2.6: Summary of chi-square analyses (after Yate's correction) of MNA estimates for males in the trappable population for each trapping session. There was no significant deviation from an anticipated ratio of 1:1 at any time.

TRAPPING SESSION	SEASON	MALES (MNA)	PROPORTION OF MNA	TOTAL (MNA)	χ^2	P
1	DISPERSAL	13	0.50	26	0.038	>0.5
2	DISPERSAL	12	0.55	22	0.038	>0.5
3	DISPERSAL	10	0.53	19	0.000	>0.9
4	WINTER	6	0.38	16	0.560	>0.1
5	WINTER	5	0.31	16	1.560	>0.1
6	WINTER	5	0.31	16	1.560	>0.1
7	WINTER	5	0.31	16	1.560	>0.1
8	WINTER	5	0.31	16	1.560	>0.1
9	WINTER	6	0.35	17	0.940	>0.1
10	BREEDING	14	0.56	25	0.160	>0.5
11	BREEDING	15	0.60	25	0.640	>0.1
12	BREEDING	10	0.62	16	0.280	>0.5
13	BREEDING	9	0.56	16	0.060	>0.5
14	BREEDING	5	0.36	14	0.640	>0.1
15	BREEDING	6	0.50	12	0.080	>0.5
16	DISPERSAL	9	0.45	20	0.050	>0.5
17	DISPERSAL	9	0.53	19	0.000	>0.9

2.6 Trappability

2.6.1 Introduction

It was apparent early in the study that the number of individuals being captured was relatively low and difficulties would arise in the accurate assessment of differential habitat use because of small sample sizes. However, the total number of captures of these individuals was consistently high. Captures can be legitimately compared for each heterogeneous habitat group to provide an indicator of activity if it can be demonstrated that individuals of each sex are equally likely to be caught. This section details the procedures involved in testing for equal trappability. Additionally, this analysis provides information on whether a sex bias in trappability was evident at any time of the year.

2.6.2 Tests for equal trappability and estimations of animal abundance and density

- *equal trappability*

The use of capture-mark-recapture (CMR) methods to estimate population size is widespread in animal studies. There is a large literature on the models designed to analyse CMR data with important recent reviews offered by Seber (1986) and Pollock *et al.* (1989). All such models make assumptions about trappability, notably that all animals in a population have the same probability of being captured in any given sample. There is, however, considerable evidence that such an assumption is not necessarily valid. The probabilility that an individual will be captured at any given trap point depends on several factors including individual trap efficiency, the likelihood that an individual will encounter the trap and the individual's response when encountering the trap (Smith 1968).

Traps were not modified in any way and were kept in good condition and so trap efficiency can be assumed to be constant throughout the study.

Traps were spaced 20m apart in a square grid pattern. This meant that, assuming random movement, any individual with a range exceeding 400 square metres should encounter a trap.

The behavioural response of individuals when encountering a trap may be dependent on sex, age, individual experience of traps, habitat features,

climate and season, as well as abiotic factors such as trap position, space between traps or trapping interval. In a study of small mammal distributions, Kikkawa (1964) summarized the principal interactions of such variables (Figure 2.4). Clearly, these interactions influence individual trappability and apparent non-random sampling must be taken into account when choosing an appropriate population estimation model for CMR data analysis.

Several tests have been proposed to determine whether capture probabilities can be assumed to be equal. Roff (1973) reviewed the most common of these methods. He showed that these tests were unable to distinguish between populations in which capture probabilities were truly random and those populations which consisted of more than one class of individual where each individual class differed in its mean trappability.

Caughley (1977) suggested that although a significant result from any trappability test could be interpreted as an indication of unequal trappability a non-significant result did not necessarily imply equal trappability. He recommended that CMR analysis only be applied to those data for which unequal trappability could not be demonstrated.

In this study, equal individual trappability could not be assessed with the conventional tests examined by Roff (1973). Insufficient data were collected for Leslie's (1958) test for equal catchability (MNA must exceed 20: Roff 1973). Sampling efficiencies (i.e., mean number of times animals are caught each session: see Figure 2.5) were too high for capture frequencies to approximate a zero-truncated Poisson distribution (Eberhardt 1969). A zero-truncated binomial distribution was also inappropriate because of possible stratification of capture probabilities by sex or age classes within the population (Roff 1973).

Many small mammals are thought to show increased capture probabilities after first capture (Tanaka 1980). Figure 2.5 shows capture frequencies for all residents in the study. An individual was classed as a resident if trapped during three or more of the 17 trapping sessions. A 'trap-happy' response was evident for 22 of the 29 residents, where 100% trap success (i.e., caught 4 out of 4 nights) was recorded at least once.

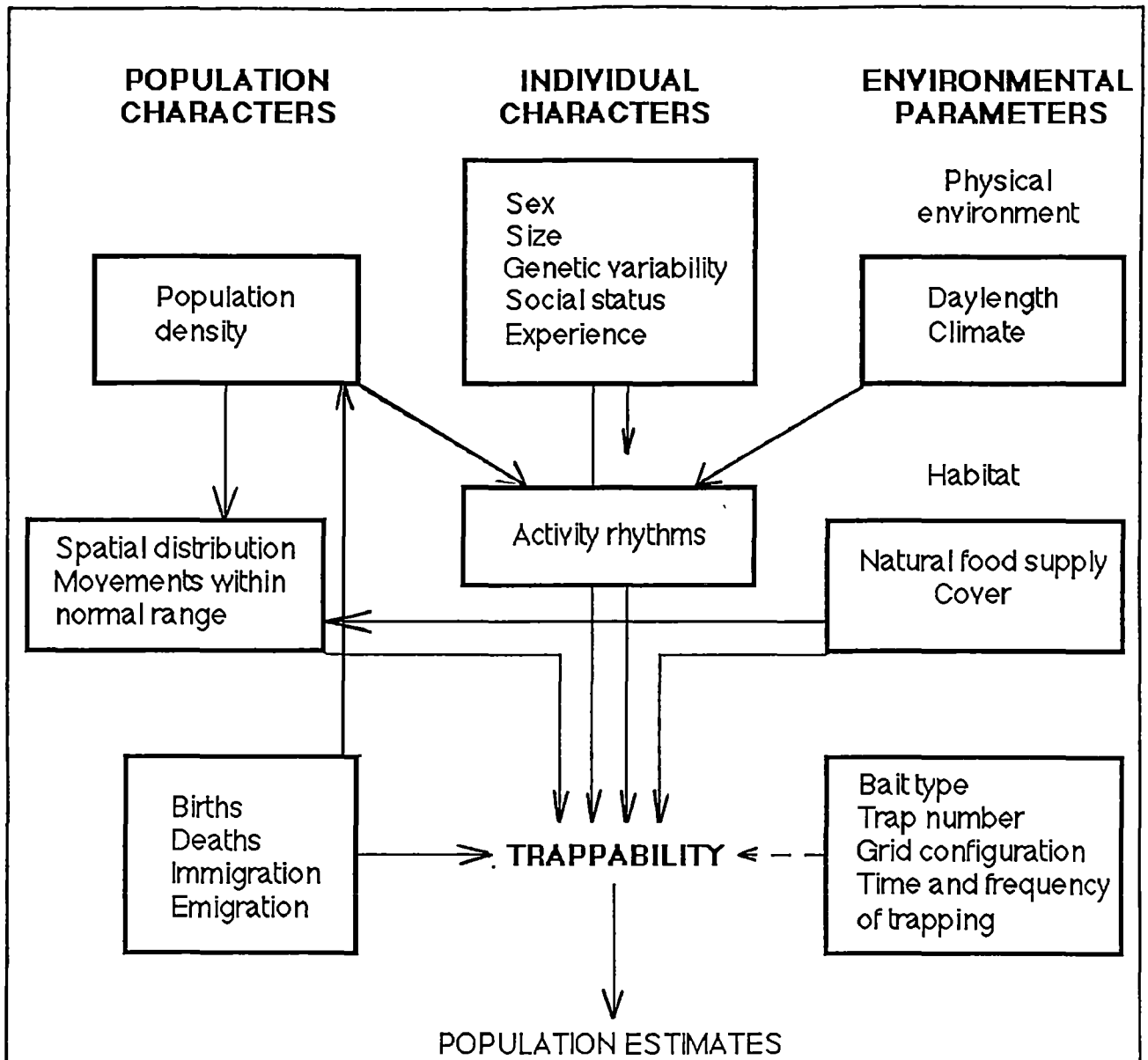


Figure 2.4: Some variables affecting the trappability of small mammals. (Arrows indicate the direction of biases which may influence population estimates: after Kikkawa 1964.)

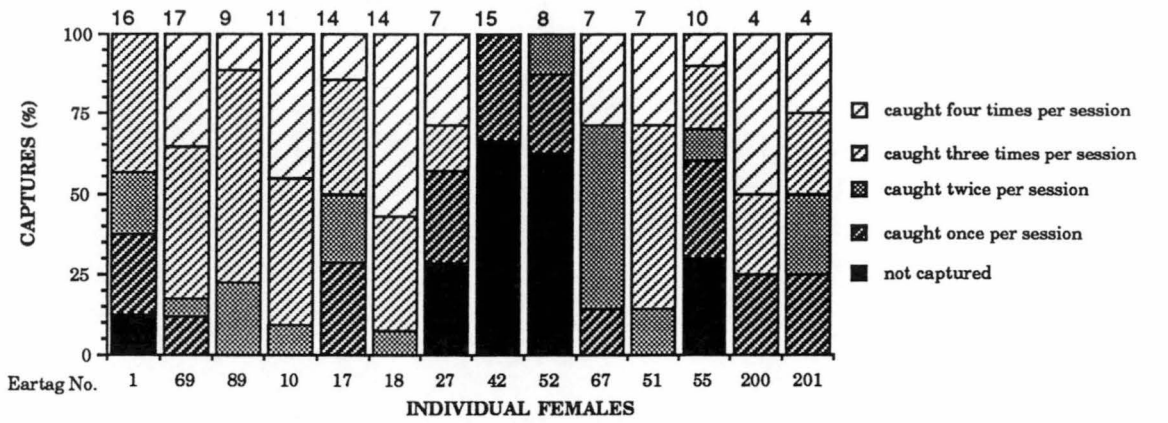


Figure 2.5a: Breakdown of captures for resident females throughout the study (Numbers above histogram denotes the number of sessions each individual was known to be alive [max. 17 sessions]).

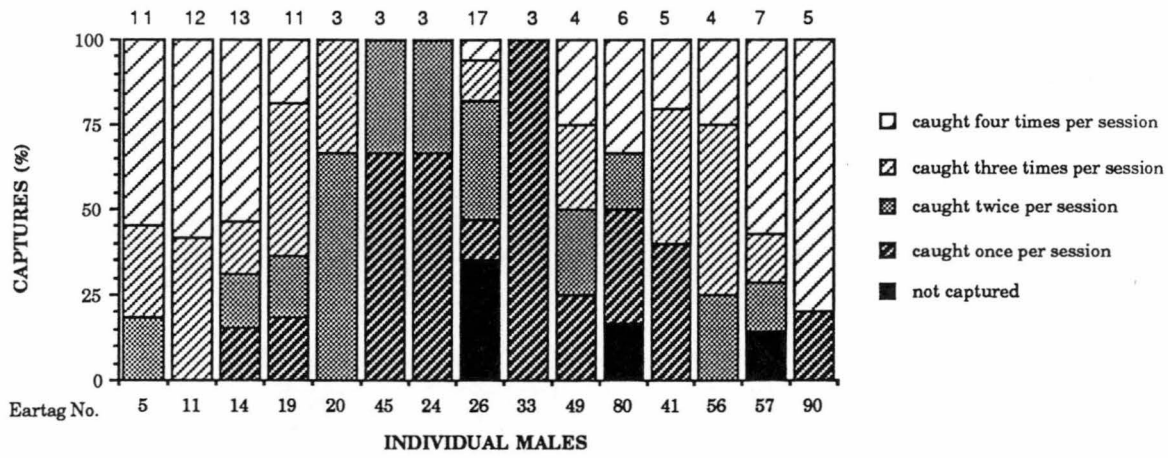


Figure 2.5b: Breakdown of captures of resident males throughout the study (Numbers above the histogram denotes the number of sessions each individual was known to be alive [max. 17 sessions]).

- abundance

Given that it is likely, although undemonstrated, that trappability of *R. l. velutinus* in this study was not equal and that there was a tendency for a 'trap-happy' response in many resident animals, it was decided that statistical estimates of animal numbers such as those involved in open-population models (e.g., Jolly-Seber) were inappropriate. Instead, the direct enumeration method outlined by Krebs *et al.* (1969) was chosen and population was assessed using minimum numbers known to be alive (MNA). The MNA estimate at any time T_i is determined by adding the number of animals (N_i) captured at T_i to the number caught before and again after T_i but not at T_i ($=Z_i$). Thus: MNA at $T_i = N_i + Z_i$. Although known to underestimate populations, this method was shown by Hilborn *et al.* (1976) to be reliable when the mean probability of capture for individuals of five species of *Microtus* was above 0.5. Tamarin *et al.* (1984) recommended direct enumeration when the number of individuals caught was a consistently high proportion of MNA. In this study, this parameter always exceeded 0.75 (monthly average 0.89).

Trappability data for all residents captured during the study are presented in Figure 2.6.

- population density

A trapping grid without discrete natural boundaries results in the taking not only of individuals which live mainly within its confines, but also those which live mainly outside the grid, but have some part of their range overlapping it. This problem of 'edge-effect' means that densities cannot be assessed directly by dividing MNA on the grid by its area. For the purposes of this study, half the distance between traps (i.e., 10m) was added to each boundary to increase the assumed sampling area from 3.24ha to 4ha (Stickel 1954). Figure 2.7 shows densities for each session expressed as MNA/ ha.

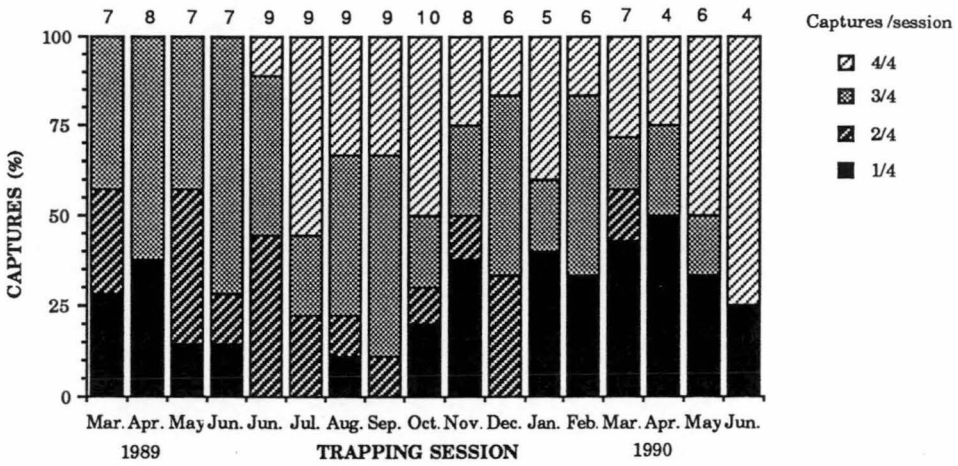


Figure 2.6a: Number of captures of resident females for each trapping session. (Number denotes residents in sample.)

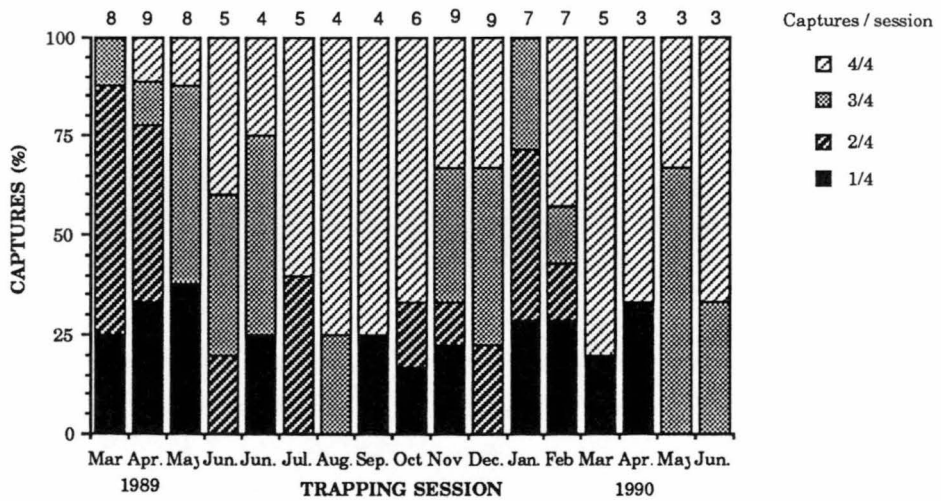


Figure 2.6b: Number of captures of resident males for each trapping session. (Number denotes residents in sample.)

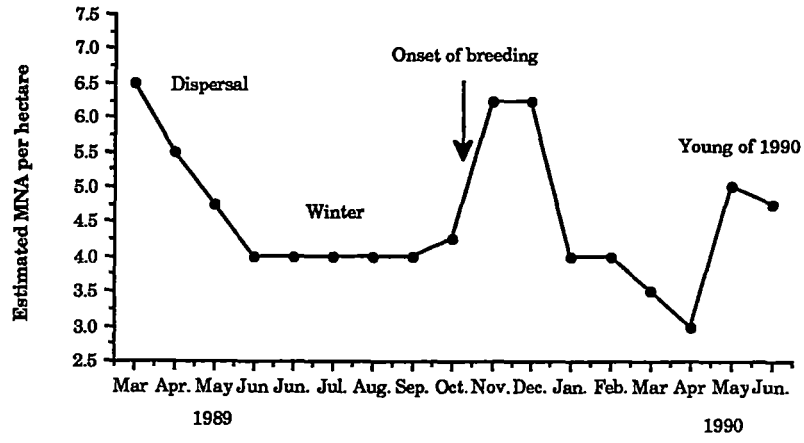


Figure 2.7: Estimated densities of *R. l. velutinus* for each trapping session (MNA.ha^{-1}).

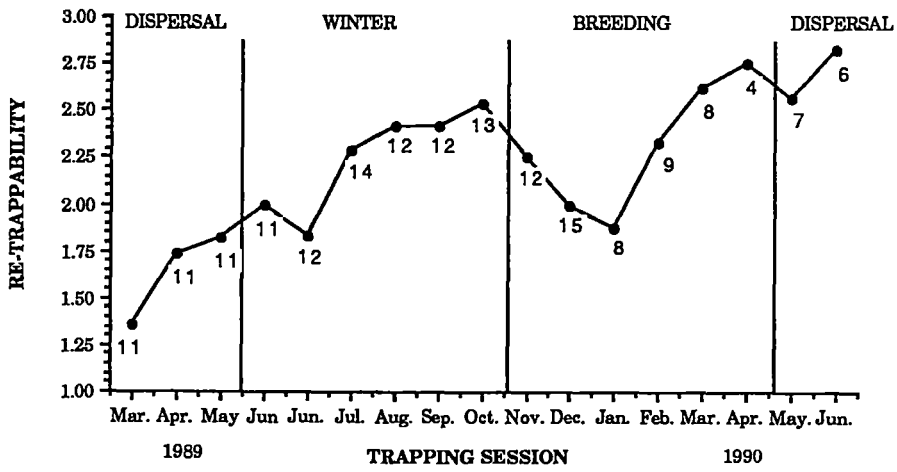


Figure 2.8: Re-trappabilities for each trapping session expressed as the total number of resident recaptures / total no. of residents (shown below data point: method after Varty 1987).

2.6.3 Variation in re-trappability

Despite not knowing whether all animals in a population are equally trappable, information regarding the re-trappability of individuals caught in a trapping study is important. Unequal re-trappability due to sex, age, season or previous capture history may lead to incorrect conclusions being drawn about habitat use.

Chi-square analyses were used to test whether individuals in the trappable population had recapture probabilities correlated with sex, age, season or previous capture history.

Expected frequencies were determined after the method used by Varty (1987). From a null hypothesis of equal re-trappability, the expected frequency of captures in any category i (E_i) was given by:

$$E_i = (X_i/T_i) \,.\, C_i,$$

where X_i = number of individuals in category i, (i.e., sex, age etc.),
T_i = number of individuals in all categories
C_i = total number of captures in all categories.

Expected and observed frequencies were compared after the application of Yate's correction for continuity for one degree of freedom (Sokal and Rohlf 1969).

- sex and age

Table 2.7 presents results of chi-square analyses by sex for all sessions and by age for 12 of 15 sessions. At the onset of breeding, all previously unmarked animals caught in reproductive condition were assigned to the adult class; all sub-adults trapped on the grid over winter but now in breeding condition were re-assigned to the adult class at the same time.

None of the comparisons by either sex or age showed any significant difference in the rate of recapture.

Table 2.7: Chi-square analyses for equal re-trappability of sex and age classes.

TRAPPING SESSION	DATE	MALE vs. FEMALE ADULT vs. SUB-ADULT →			
		χ^2	Sig.	χ^2	Sig.
	Dispersal				
1	20.iii.89	1.558	n.s.	0.658	n.s
2	3.iv.89	0.212	n.s.	0.004	n.s.
3	1.v.89	0.009	n.s.	0.002	n.s.
	Winter				
4	29.v.89	0.238	n.s.	not analysed*	
5	26.vi.89	not analysed		0.000	n.s.
6	24.vii.89	0.183	n.s.	1.839	n.s.
7	21.viii.89	not analysed		0.011	n.s.
8	18.ix.89	not analysed		not analysed	
9	16.x.89	0.001	n.s.	0.005	n.s.
	Breeding				
10	13.xi.89	0.002	n.s.	all adults	
11	11.xii.89	0.139	n.s.	all adults	
12	8.i.90	0.046	n.s.	all adults	
13	5.ii.90	0.001	n.s.	not analysed	
14	5.iii.90	1.765	n.s.	not analysed	
15	2.iv.90	not analysed		not analysed	
	Dispersal				
16	30.iv.90	0.008	n.s.	0.776	n.s.
17	28.v.90	0.003	n.s.	1.534	n.s.

* Not analysed because expected frequencies were less than five; n.s. = not significant

Table 2.8: Chi-square analyses for equal re-trappability based on previous capture history.

TRAPPING SESSION	DATE	CAUGHT BEFORE vs. CAUGHT FIRST TIME	
		χ^2	P
	Dispersal		
1	20.iii.89	not applicable	
2	3.iv.89	not analysed*	
3	1.v.89	not analysed	
	Winter		
4	29.v.89	not analysed	
5	26.vi.89	not analysed	
6	24.vii.89	not analysed	
7	21.viii.89	not analysed	
8	18.ix.89	not analysed	
9	16.x.89	not analysed	
	Breeding		
10	13.xi.89	2.380	n.s.
11	11.xii.89	not analysed	
12	8.i.90	not analysed	
13	5.ii.90	not analysed	
14	5.iii.90	not analysed	
15	2.iv.90	not analysed	
	Dispersal		
16	30.iv.90	4.170	P<0.05
17	28.v.90	2.620	n.s

* Not analysed because expected frequencies were less than five; n.s. = not significant

- previous capture history

The effect of previous capture history on re-trappability could only be tested on data from three trapping sessions since expected frequencies in the smallest class were often less than five. At the onset of breeding, a large influx of unmarked animals was recorded. No significant difference in the re-trappability of these adults was detected when compared with residents (χ^2=2.38, d.f=1, P>0.1,).

Data from two more sessions were also tested. These sessions coincided with the time when most young of the year entered the trappable population (April and May 1990). A significant difference in recapture rates was recorded when young of the year were compared with adults in April 1990 (χ^2=4.17, d.f.=1, P<0.05). A similar, but not statistically significant, trend was observed in May 1990 (χ^2=2.62, d.f.=1, P<0.1: Table 2.8). At this time, young are dispersing to establish their own ranges. Such activity may result in fewer recaptures of individuals as they pass through different parts of the grid.

- season

In Section 2.7 (below), the trapping study is divided into three seasons defined as dispersal, winter and breeding. Sampling effort (100 traps set for four nights: Section 2.2) was constant throughout the study with the expectation that mean recaptures of individuals would remain the same for each trapping session. Any deviation may be explained by seasonal effects. Because the dispersal seasons each contained fewer trapping sessions than the winter and breeding seasons, comparisons have been confined to differences between winter and the breeding season. Figure 2.8 shows a rise in re-trappability before the onset of breeding when the number of individuals in the trappable population increased. During winter (six trapping sessions), four resident males were trapped readily (83 of a possible 96 times: 3.5±0.8 captures per session); nine resident females were trapped on 154 of 216 occasions (2.85±0.63 captures per session: t=1.004, d.f.=4, P>0.3). Trappability decreased during the breeding season but did not differ significantly by sex (t=0.496, d.f.=5, P>0.5).

2.6.4 Odour bias

- Introduction

Residual odours from previous occupants of live traps may influence trap entry in some small mammal species (Boonstra and Krebs 1976; Stoddart 1982; Stoddart and Smith 1984). Individual response may vary within species depending on sex and reproductive status.

R. l. velutinus is a semi-solitary rodent which uses olfaction as a means of communication between widely spaced individuals. Mallick (1989) reported that in laboratory trials males and females made clear choices about trap entry. When individuals were placed singly in an arena and given the choice of entering a clean trap or one which had soiled bedding, a strong preference for the dirty traps was recorded. Mallick (1989) also showed that if an individual was given a choice between a trap soiled by a male and a trap soiled by a female, individuals of both sexes avoided female-scented traps, preferring male-scented traps.

As noted earlier (Section 1.3.1), the principal aim of this study was to investigate a reported decline in the proportion of males in a trappable population over winter. If males in free-living populations were avoiding traps scented with female odour then this would offer an explanation for fewer male captures at this time. Traps were only removed for cleaning at the end of a trapping session so the possibility of a preference for dirty traps or an avoidance of dirty female traps warranted examination.

- Methods

To test odour bias in the field, trapping was undertaken during the breeding season (4 - 8 December 1989) and in mid-winter (30 July - 8 August 1990) outside the normal pattern of monthly sampling. Forty traps were set along the four most westerly grid rows (4 x 10 configuration) in the manner described previously (Section 2.2). When an individual *R. l. velutinus* was captured and the trap soiled, a clean trap was placed alongside the dirty one to give the next individual a choice between either a clean or a dirty trap. Relative position was determined by the toss of a coin. If a trap station had two dirty traps after a choice had been made, one trap was replaced with a clean one and the dirty trap was coupled with a clean one at a trap station

starting in the fifth grid row.

- Results and discussion

Only clear choices were analysed in this experiment. Paired trap stations with an animal in each trap were found 11 times in December 1989 and once in August 1990. These results were discarded as conclusions about which animal had entered which trap first could not be made. A total of 39 clear choices were made by individuals in December 1989 in 254 paired trap nights. In winter 1990, 42 choices were made in 270 paired trap nights. The results are presented in Table 2.9. No obvious preference for dirty or clean traps by either sex was apparent.

No avoidance of female-soiled traps by males or females was apparent in winter (Table 2.10). Insufficient data prevented analysis during December 1989 but at this time males were actively seeking mates and an avoidance of female odour would be unlikely.

Although the effects of odour on social spacing in free-living populations of *R. l. velutinus* are unknown, it appears from these data that individuals are equally likely to enter a dirty trap as a clean one. Odour bias, then, is unlikely to explain a reduction in the proportion of males in a trappable population during winter.

2.7 Life history

Information gathered during this study can be used to construct a life history for *R. l. velutinus*. Figure 2.9 shows a the occurrence of different age classes in the population during the study.

A period of dispersal was evident during the two preliminary and the first investigative trapping sessions (March - May 1989). Young of the year were numerous and adults in reproductive condition were observed.

In June 1989, the MNA estimate for the trappable population declined to 16, a number which persisted through winter. Adults caught in June 1989 were no longer in breeding condition. Previously unmarked individuals entering the trappable population during winter could only be classed as adult and sub-adult by size and reproductive characters. Consequently, all sub-adults and juveniles were grouped together as young of the year.

Table 2.9: Observed and expected capture frequencies for *R. l. velutinus* based on clean or dirty traps (Expected frequencies refer to random trap entry).

TRAP CHOICE ON DAY i	CAPTURES ON DAY i + 1			
	MALES		FEMALES	
	OBSERVED	EXPECTED	OBSERVED	EXPECTED
BREEDING SEASON				
SOILED	9	12	8	7.5
CLEAN	15	12	7	7.5
	24	24	15	15
	χ^2=1.042	P<0.5	χ^2=0	P>0.9.
WINTER				
SOILED	14	11.5	10	9.5
CLEAN	9	11.5	9	9.5
	23	23	19	19
	χ^2=3.522	P>0.1	χ^2=0	P>0.9

Table 2.10: Observed and expected capture frequencies for *R. l. velutinus* based on sex (Expected frequencies refer to random trap entry).

TRAP CHOICE ON DAY i	CAPTURES ON DAY i + 1			
	MALES		FEMALES	
	OBSERVED	EXPECTED	OBSERVED	EXPECTED
BREEDING SEASON				
SOILED FEMALE	1	2.5	1	2
CLEAN	4	2.5	3	2
	5	5	4	4
	Not tested - Expected frequencies < 5.			
WINTER				
SOILED FEMALE	4	4	6	6
CLEAN	4	4	6	6
	8	8	12	12
	χ^2=0.062	P>0.5	χ^2=0.062	P>0.5

At the onset of breeding when all males trapped had fully scrotal testes, no conclusions about the year of their birth could be made for previously unmarked individuals and all were classed as adults.

The winter season (six sessions between 30 May and 20 October 1989) was characterized by regular trapping of residents (Section 2.6.3). Three young and one adult male accounted for 91% of all male captures (4 residents caught 83 times; 3 transients caught 8 times). Nine resident females were captured 154 times (97.5%). Two transient young were caught six times.

The breeding season (six sessions between 13 November 1989 and 6 April 1990) commenced with a number of previously unmarked individuals being captured. The winter residents continued to be caught throughout the breeding season (Table 2.5) although less frequently. Mean male body weight had risen sharply, and in October 1989 a significant difference was apparent between sexes ($t=4.11$, 10 d.f., $P<0.01$). This was the only time that such a difference was recorded.

The MNA estimate for males rose from six in October to 14 in November 1989. Re-trappability for resident males caught at least twice in a session fell from 12 recaptures for four individuals in October (i.e., all animals caught on every occasion; mean=3.0±0.0) to a mean of 2.1±0.8 (1 S.D.:n=9) recaptures per individual in November 1989 ($t=3.5$, 9 d.f., $P<0.01$). At the same time, mean captures for females fell from 2.5±0.8 (n=8) to 2.2±0.8 (n=5) ($t=0.651$, 7 d.f., $P>0.5$).

The significant decline in the recapture rate for males at this time may reflect, among other things, an alteration in the range size of individuals. During winter, ranges may be relatively small. The onset of breeding may result in an expansion of ranges as potential mates are sought. Such behaviour may result in residents spending less time on the grid. It is noteworthy that resident males trapped over winter continued to be trapped well into the breeding season (Table 2.5). Unmarked individuals which first appeared in the trappable population at the onset of breeding also tended to remain. It is interesting to speculate that at this time of the year, even though males are actively seeking potential mates, they may be maintaining a core area within their individual range rather than roaming haphazardly. In some polygynous mating systems, males are known to roam widely in

search of females (Trivers 1972) but little is known of whether males continue to maintain an area of territory. In this study the maintenance of such a core is supported by the persistence (but declining recapture rate) of the winter residents into the breeding season and the large influx of previously unmarked males (of similar re-trappability) whose ranges now overlap some part of the grid. A study incorporating both live-trapping and radio telemetry would be useful in assessing such speculation.

The 1990 dispersal season overlapped the breeding season, commencing at the time of first capture of a young individual (7 February 1990) and continuing until the end of the study. An expected influx of juveniles coinciding with weaning in February and March 1990 did not occur. Only three female young of the year were captured between February and May 1990 when a further 10 young of the year were trapped. Mean body weight for the 10 new individuals was 68±9g. This differed significantly from the mean weights of the individuals trapped earlier (86±1: $t=5.91$, 9 d.f., $P<0.001$). These animals were deemed to be from second litters. The absence of equivalent numbers of individuals from first litters is puzzling. Lactating females were first observed in December 1989. Given that young are independent between 22 and 25 days (Green 1967; Fox 1979a) and usually enter the trappable population at five weeks of age (Taylor and Horner 1973), the occurrence of juveniles in February/ March was expected. Their absence from the trappable population remains incompletely explained. There was less-than average rainfall during November and December 1989. This may have had an adverse effect on the lactational abilities of the females due to a reduction in available food (i.e., the number of fruiting plants or a delay in the flush of insects expected at this time). Rainfall for a similar period in 1988 was more constant (Figure 2.10) and the number of young from early and later litters at the start of the study was more even.

2.8 Discussion

It was not possible to make conclusions about equal trappability for all *R. l. velutinus* since there was no way of knowing how many individuals, for whatever reason, did not enter traps. However, *R. l. velutinus* appears to be a species which is re-trapped readily irrespective of sex, age, season or

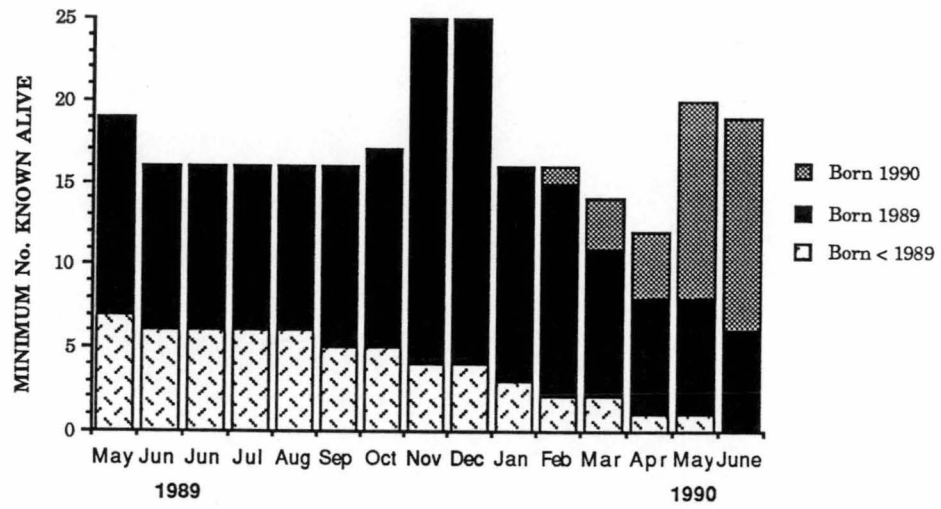


Figure 2.9: The age classes of individuals in the trappable population during the study.

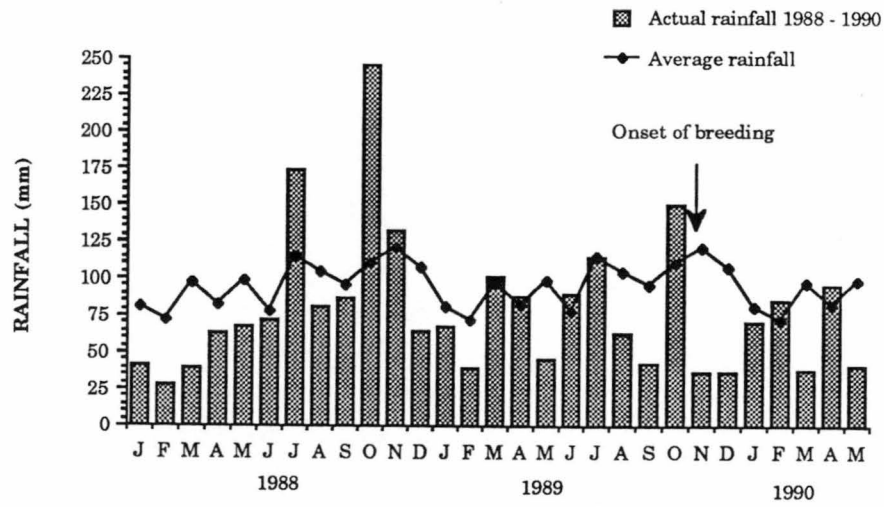


Figure 2.10: Rainfall data for Fern Tree (1988-1990).

previous capture history. Additionally, no bias could be detected based on the response of individuals to prior occupancy of traps.

Statistically significant between group differences were only recorded for two comparisons: when young of the year first entering the trappable population in 1990 were compared with adults at the same time; and when the number of recaptures of male residents in the last winter session (October 1989) was compared with the recapture rate for resident males in the first session of the breeding season (November 1989). Between-sex and between-age comparisons for each session did not differ significantly (Table 2.7) and so the decision to use total numbers of captures rather than the total number of individuals as an indication of habitat preference (see Chapter 4) appears justified.

The data presented above provide answers for some of the questions posed at the beginning of the study. Principally, although a trend towards fewer males in the trappable population was evident during winter, at no time did the sex ratio based on the MNA estimate differ significantly from parity (Table 2.6).

The sex ratio of most mammal populations is often thought to approach unity at birth (or more precisely at conception). However, in a recent review of sex ratio variation, Cockburn (1990) emphasized the tendency in some species for male offspring to disperse, while female young tended to settle adjacent to, or in some instances, in their mother's home range. This leads to local resource competition between mothers and daughters and it was suggested that a selective advantage could be gained by investing in fewer female offspring (i.e., a male-biased sex ratio at birth). This hypothesis was supported by data from primates (Johnson 1988), rodents (Caley *et al.* 1988) and deer (Clutton-Brock *et al.* 1982).

However, evidence is also available for secondary sex ratios biased towards fewer males. Differential mortality within age classes can affect the ratio of individuals surviving to maturity. Trivers (1972) reviewed the relevant literature and concluded that in cases where a sex ratio was unbalanced it was usually biased towards fewer males. The implication was that males tended to suffer higher mortality rates than females. This was attributed to increased predation and an increased susceptibility to disease

when males were establishing their own range.

I use the reviews of Trivers (1972) and Cockburn (1990) to illustrate the complexities involved in the debate about primary and secondary sex ratios. In this study, sample sizes were too small to derive any useful information about sex ratio variation in *R. l. velutinus*. It is very difficult to determine accurately from a field-based study what the anticipated secondary sex ratio is at any given time, even if an assumption of parity at birth is made.

However, the sample size does not preclude comparisons with the data provided by Stoddart and Challis (Table 1.1). In six trapping sessions during the 1987 winter, they trapped 11 females and two males (χ^2=4.293, d.f.=1, P<0.05). By expanding the size of trapping grid and therefore increasing the number of individuals in the trappable population, it was possible to show an equal sex ratio for all individuals in the trappable population during the six sessions of the 1989 winter (7 males: 12 females; χ^2=0.84, d.f.=1, P>0.1).

The significant difference in male and female number observed by Stoddart and Challis was most likely a product of their grid size. As grid size increases it is probable that the overall sex ratio will approach parity.

To summarize, no significant deviation from a balanced sex ratio was found in this study although a trend to fewer males in winter was apparent. Overall, individuals within the trappable population were equally likely to be captured irrespective of sex, age, season, previous capture history or prior trap occupancy.

CHAPTER THREE
HABITAT ANALYSIS

3.1 Introduction

Many studies of small mammal habitat utilization have emphasized the importance of the physical habitat in determining animal distributions (see Section 4.1). Increasingly, multivariate statistical analyses of plant communities are being incorporated in such studies.

While most investigators recognize the temporal as well as the spatial dynamics of communities, a vegetation classification is sometimes extrapolated and afforded the status of an entire ecosystem classification, even though the data were recorded *at a single point in time*. Recognition of successional processes and vegetational change is essential for a complete understanding of patterns and variations in vegetation groups. In a review of analytical techniques used between 1960 and 1986, Kent and Ballard (1988) illustrated how researchers tended to use complementary or multiple analyses to ensure that conclusions based on *static* structural and floristic characters within plant associations were accurate.

To provide a quantitative description of *R. l. velutinus* habitat, an intensive survey of variation present in the vegetation over the trapping grid was conducted. The sampling techniques and complementary analytical methods used for this study are described below and, on the basis of structural and floristic attributes, discrete habitat groups are defined.

3.2 Sampling and analytical techniques

3.2.1 Field methods

Vegetation surveys were conducted in January and February 1990. 4m x 4m quadrats, with the centre at each of the 100 trap points were established. Quadrat size was based on the concept of the minimal area/ species relation curve (*sensu* Goldsmith and Harrison 1976). This was defined as the smallest quadrat size on which representative information about species composition could be based (see Appendix 1).

Vascular plant species rooted in, or projecting into, each quadrat were

recorded at each of seven height classes (0-20cm; 21-50cm; 51-100cm; 1-2m: 2-5m; 5-10m; >10m). A visual estimate of the total cover of each stratum was made using a Braun-Blanquet scale (Mueller-Dombois and Ellenberg 1974). The cover afforded by large (>10cm diameter) rocks and decaying logs was also estimated in each quadrat. Slope and aspect were recorded at each trap station using a compass and clinometer.

Taxonomic nomenclature for all species follows Buchanan, McGeary-Brown and Orchard (1989). A complete species list is given in Appendix 2.

3.2.2 Multivariate analyses

Floristic and structural data were stored on the ecological data base system ECOPAK (Minchin 1986). Two-way indicator species analysis (TWINSPAN: Hill 1979a) was used to combine structural and floristic attributes to provide a quantitative description of plant assemblages and to define the habitat groups. TWINSPAN is a polythetic-divisive technique which produces a robust, two-way arranged hierarchical matrix. Analyses begin with all available data in a single cluster. This is successively divided, first ordinating data by reciprocal averaging and then splitting samples at the centre of the reciprocal average axis. In contrast, polythetic-agglomerative procedures separate all data and then group similar attributes together and progressively compile an upwards hierarchy. A major advantage of divisive techniques is that all available information is used when making the critical topmost divisions (Lambert *et al.* 1973) and so the likelihood of spurious groupings is diminished. When contrasted with other hierarchical (both divisive and agglomerative) procedures, TWINSPAN was rated as consistently and significantly distinct from the other methods (Gauch and Whittaker 1981).

Vegetation types and physiographic features were ordinated using detrended correspondence analysis (DCA) to determine relationships between habitat variables. These analyses were conducted using the FORTRAN procedure DECORANA (Hill 1979b). Ordination by DECORANA arranges samples in an objective order with sites of most similar composition occurring most closely together. To minimize the influence of rare species (i.e., occurring in only one quadrat), the DECORANA

'downweighting' option was invoked, which reduces the abundance of rare species in proportion to their frequency (Hill 1979b).

3.3 Results

From the TWINSPAN classifications, three habitat groups were selected at levels that were ecologically meaningful. Ordination by DECORANA resulted in the further division of Group 1 into two sub-groups (Figure 3.1). The location of each of these habitat groups in the trapping grid is shown in Figure 3.2. A dendrogram depicting their hierarchical relationships is presented in Figure 3.3.

Species occurring in more than 40% of quadrats in any one TWINSPAN group are summarized in Table 3.1. The frequency of occurrence of all species is shown in Appendix 3. Table 3.2. shows the major physiographic features of the trapping grid. The frequency of occurrence of all habitat variables in each TWINSPAN group is presented in Appendix 4.

Confirmation of the TWINSPAN classifications was obtained from an ordination of structural and floristic attributes using DECORANA (Hill 1979b). It must be emphasized, however, that these groups are not discontinuous. Figure 3.4 illustrates the continuous nature of the variation in vegetation. Scores on Axis 1 can be interpreted as following a gradient from a wet sclerophyll association (low DCA scores) through to a drier, more open form (high DCA scores). Quadrats surveyed in the wettest regions such as are found in habitat groups 1a and 1b correspond to the lowest scores. DCA scores on Axis 2 approximate the topography and geology of the study area. The highest scores correspond to traps located on the outcrop of dolerite boulders along the grid's northern side (Habitat group 2).

The general attributes of each habitat group are described below:

- Group 1a (9 trap points: Figure 3.5)

This group corresponds with the wettest area of the grid. A dense fern understorey (*Blechnum wattsii, Dicksonia antarctica* and *Polystichum proliferum*) occurs in eight of the nine quadrats. A shrub layer of rainforest species, including *Atherosperma moschatum* and *Nothofagus cunninghamii,* occurs to approximately two metres height. Thickets of

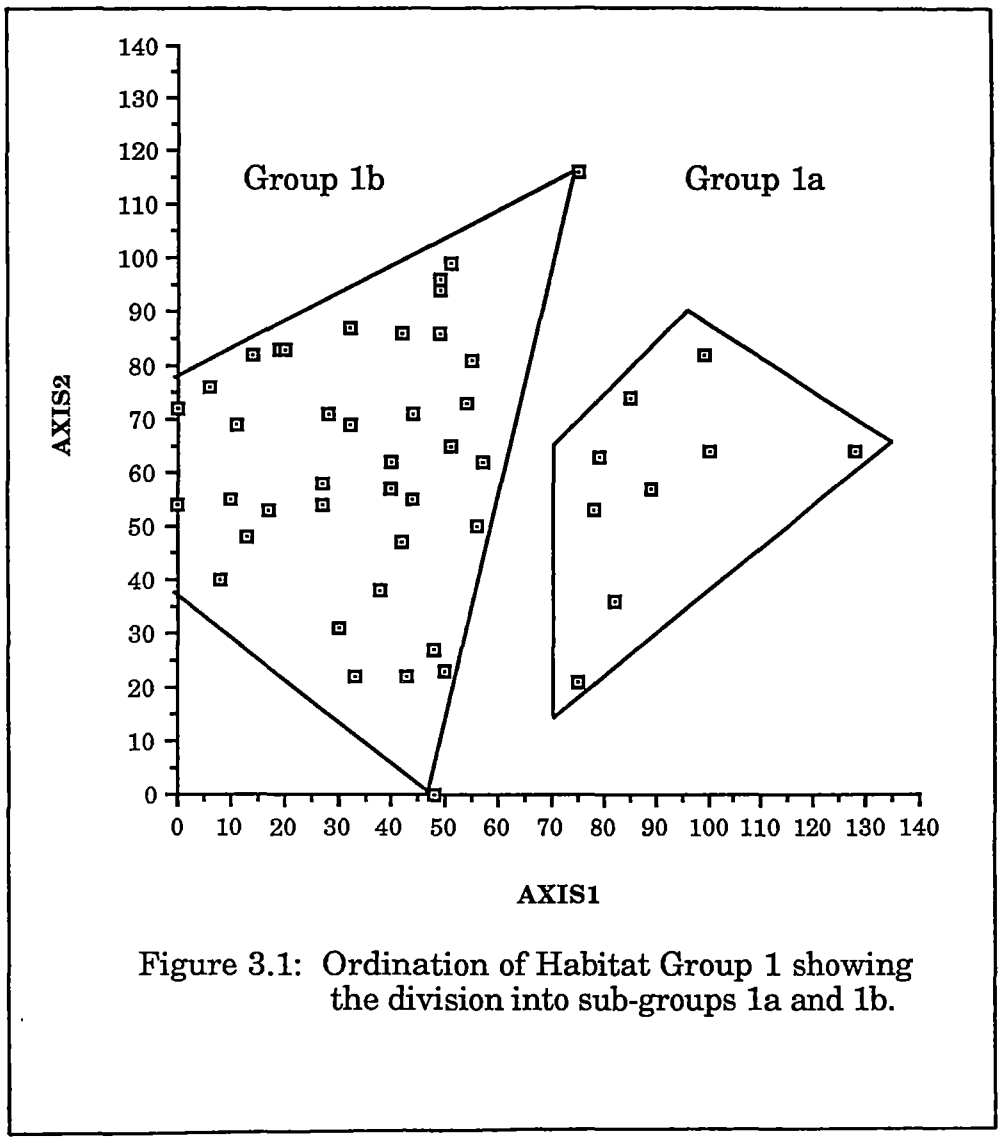


Figure 3.1: Ordination of Habitat Group 1 showing the division into sub-groups 1a and 1b.

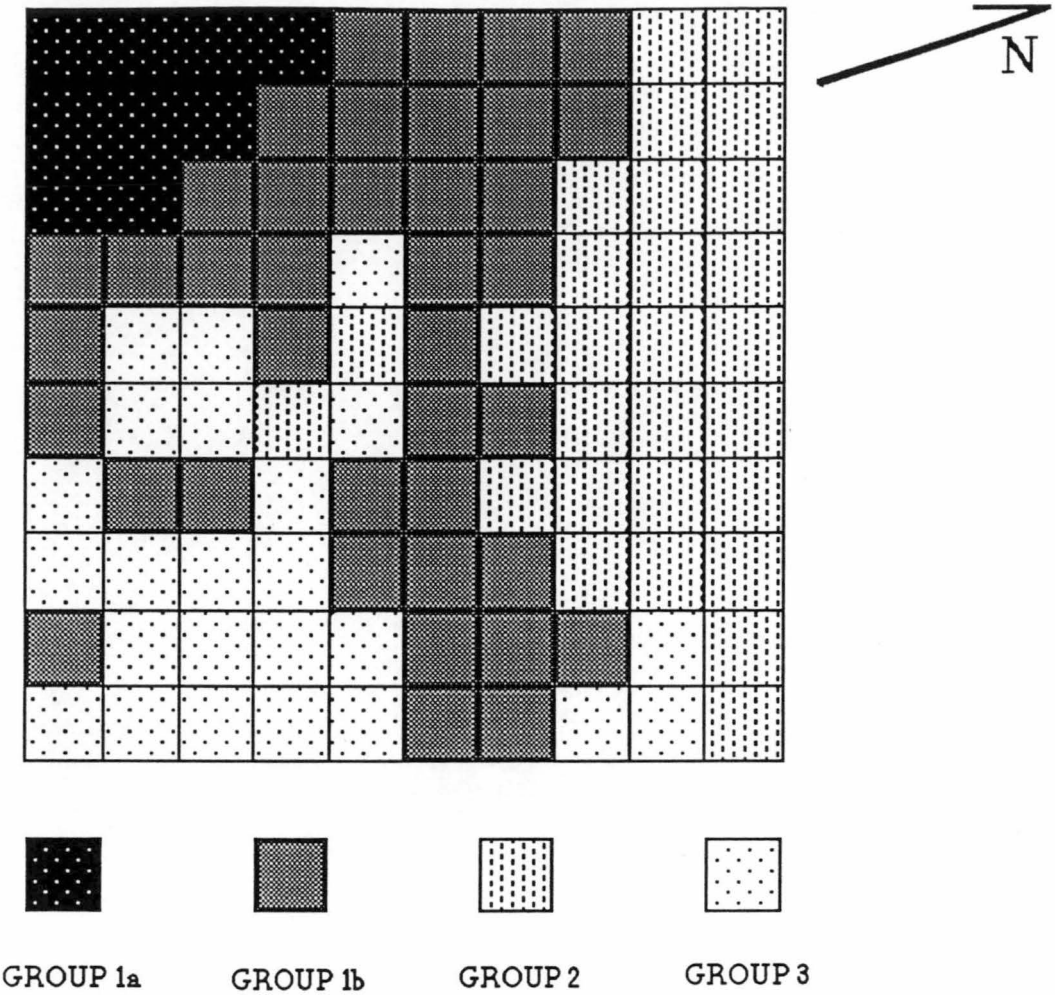


Figure 3.2: Habitat groups found within the trapping grid after classification by 'TWINSPAN' and ordination by 'DECORANA'.

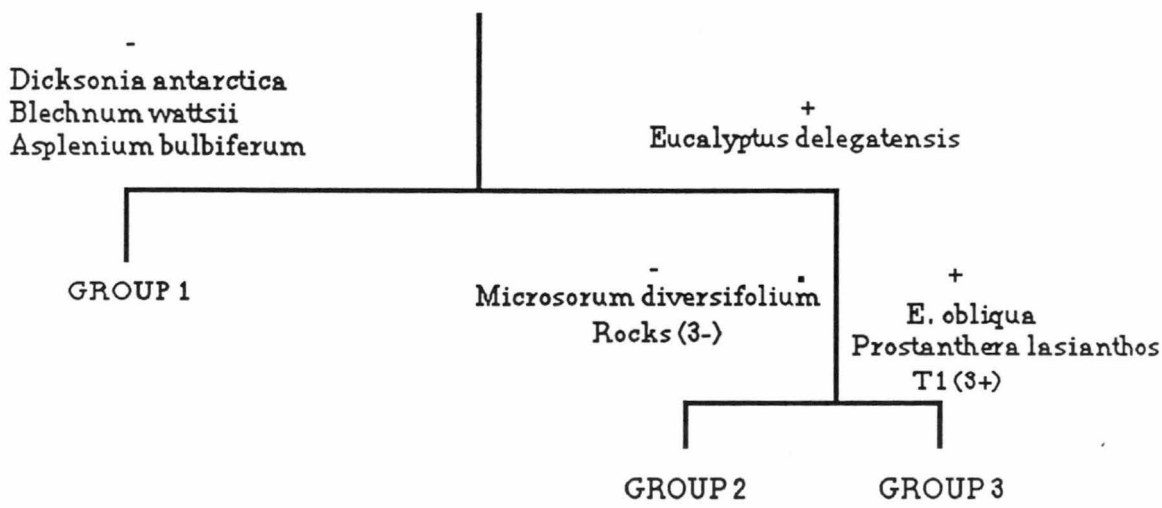


Figure 3.3: Hierarchy of 'TWINSPAN' structural and floristic associations.

Table 3.1: The frequency of occurrence of the major plant species occurring in >40% of quadrats in a TWINSPAN group. A complete list of frequencies is given in Appendix 3.

	Habitat group			
	1a	1b	2	3
Number of quadrats	**9**	**39**	**28**	**24**
Dicotyledoneae				
Eucalyptus delegatensis			++	***
Eucalyptus obliqua				*
Eucalyptus regnans	+			
Acacia dealbata			*	+
Atherosperma moschatum	*			
Bedfordia salicina	++	+++	+++	+++
Billardiera longiflora			+	++
Geranium potentilloides			***	
Olearia argophylla	++	+++	***	++
Olearia phlogopappa			*	
Pittosporum bicolor	*	*		**
Pomaderris apetala	++	+++	+++	+++
Prostanthera lasianthos				**
Senecio linearifolius			*	
Tasmannia lanceolata	***			
Monocotyledoneae				
Deyeuxia rodwayi			***	+
Drymophila cyanocarpa		*	**	***
Gahnia grandis	*			
Pteridophyta				
Asplenium bulbiferum		***		
Blechnum wattsii	++	+		
Dicksonia antarctica	++	+		
Microsorum diversifolium		**	++	
Polystichum proliferum	++	+++	+	***

*	occurs in 40-49% of quadrats in group
**	occurs in 50-59% of quadrats in group
***	occurs in 60-69% of quadrats in group
+	occurs in 70-79% of quadrats in group
++	occurs in 80-89% of quadrats in group
+++	occurs in 90-100% of quadrats in group

Table 3.2: Summary of major physiographic features occurring in each 'TWINSPAN' group.

	TWINSPAN Group		
	1	2	3
Number of Quadrats	48	28	24
Mean No.of species/quadrat	13.2±3.5(1 SD)	13.7±3.1	12.4±2.2
Average Slope	17°±6	18°±7	14°±6
Aspect	133°±23	129°±19	129°±54

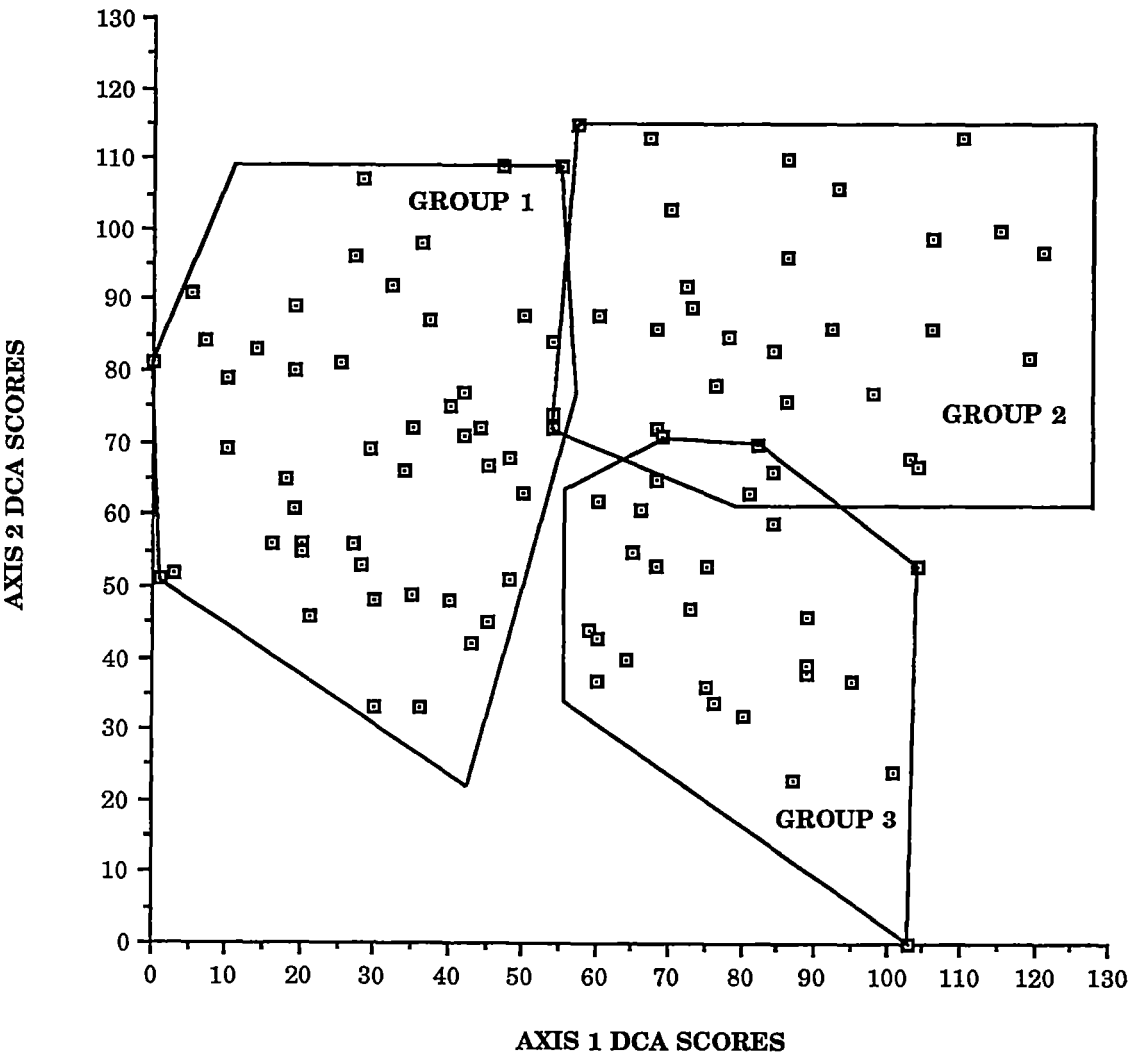


Figure 3.4: 'DECORANA' (DCA) ordination using structural and floristic data; polygons enclose all sites in the 'TWINSPAN' groups.

Gahnia grandis are found in areas of open canopy. An open overstorey of mature *Eucalyptus regnans* shades a closed sub-canopy of young *Bedfordia salicina, Pomaderris apetala* and *Olearia argophylla.* This area had an overall south easterly aspect and only received full sun for three to four hours per day in winter and up to six hours per day in summer.

- Group 1b (39 trap points: Figure 3.6)

Similar to but drier than Group 1a. Many large decaying logs are present. An underground stream with an outflow in the central portion of the grid running due east extends the area of dense fern understorey beyond the eastern edge of the grid. The steep-sided gully in which the stream flows is characterized by a sub-canopy of tall *D. antarctica.* This gully marks a distinct floristic and structural boundary between habitat groups 2 and 3.

- Group 2 (28 trap points: Figure 3.7)

The northern edge of the trapping grid with a less open overstorey dominated by *E. delegatensis.* The ground is strewn with large dolerite boulders and has a dense cover of the ferns *Microsorum diversifolium* and *P. proliferum.* The sub-canopy comprises *B. salicina, P. apetala,* and *O. argophylla,* with *O. phlogopappa, O. viscosa* and *Acacia dealbata* also present. Two grasses, *Deyeuxia rodwayi* and *Holcus lanatus,* are common. This group is on the steepest part of the grid and ends abruptly at the northern ridge of the gully above the stream.

- Group 3 (24 trap points: Figure 3.8)

An area with little or no understorey located in the south eastern corner of the grid. The sub-canopy, comprising *B. salicina, P. apetala, Pittosporum bicolor* and *Prostranthera lasianthos,* is only partly shaded by a mixed overstorey of *E. delegatensis, E. obliqua* and *A. dealbata.* Occasional pockets of *P. proliferum* can be found on and around rotting logs. This area appears to have been subjected to intense burning. It also appears as the driest part of the grid. Soil moisture indices were not recorded during the study, but, unlike areas in Groups 1a and 1b, no surface water was ever noted here during the trapping program. This area is the

Figure 3.5: Habitat group 1a. The wettest area of the trapping grid characterized by dense stands of the fern *Blechnum wattsii*.

Figure 3.6: Habitat group 1b. The dense ground cover includes *Gahnia grandis, Dicksonia antarctica* and *Polystichum proliferum.*

Figure 3.7: Habitat group 2. A dolerite boulder scree slope with a dense cover of the ferns *Microsorum diversifolium* and *Polystichum proliferum*.

Figure 3.8: Habitat group 3. A level area characterized by a dense sub-canopy of the regenerating broad-leaved species *Bedfordia salicina, Pomaderris apetala* and *Olearia argophylla.*

flattest of the study area with an overall easterly aspect. It falls away sharply into the central stream gully and also to the south, off the grid. During March 1990, *P. bicolor* and *P. apetala* saplings were observed to be wilting in seven quadrats. Such wilting was not seen anywhere else in the study area.

3.4 Discussion

Wet sclerophyll forests are responsive to local climate, substrate, drainage, aspect and fire history. In Tasmania, such communities extend over large areas where soil moisture and nutrient status is high. The canopy dominants are eucalypts which possess features promoting fire: their leaves and twigs contain volatile oils; open crowns with pendulous foliage encourage updraughts; and regular bark-shedding results in heavy litter accumulation (Ashton 1981). Changes in floristic and structural composition follow such fires. Therefore, forest structure and understorey composition, although also influenced by edaphic controls, are largely determined by past fire history (Kirkpatrick *et al.* 1988).

Fires rarely burn all areas with equal intensity and it is likely that parts of the study area were burned at different intensities in the wildfire of February 1967. Figure 3.9 shows a sequence of aerial photographs taken before and immediately after this fire and, 21 years later, in December 1988. It appears possible that some areas formerly carrying tall eucalypts are now dominated by a lower canopy consisting of *B. salicina*, *P. apetala* and *O. argophylla*. These areas have the highest abundance of fire-killed eucalypt stags and decaying logs. Few eucalypt saplings were seen to be over-topping the canopy of broad-leafed species in much of this area (habitat group 3) . The areas where the canopy appears unchanged correspond to the wettest gullies of habitat groups 1a and 1b.

As mentioned, the assemblage of communities which makes up a wet sclerophyll forest is a product of factors other than the forest's fire history. Variation in soil moisture and drainage, slope and aspect may predispose some areas to more intense burning. It should be emphasized however, that these same physiographic features will also influence community recovery after fire. For example, the wettest parts of the grid (habitat groups 1a and

Figure 3.9: Aerial photographs of the area where the trapping grid (depicted) was situated.

Figure 3.9a is a photograph taken in December 1966, i.e., prior to the February 1967 wildfire. Note the even overstorey.

Figure 3.9b is a photograph taken immediately after the wildfire. Many logs are visible, particularly in the eastern portion of the trapping area. The overstorey in the south western corner appears less affected by fire.

Figure 3.9c is a photograph taken in December 1988. The eastern part of the trapping grid shows a thick sub-canopy of regenerating broad-leaved species. The south western corner shows an overstorey dominated by *Eucalyptus* spp.

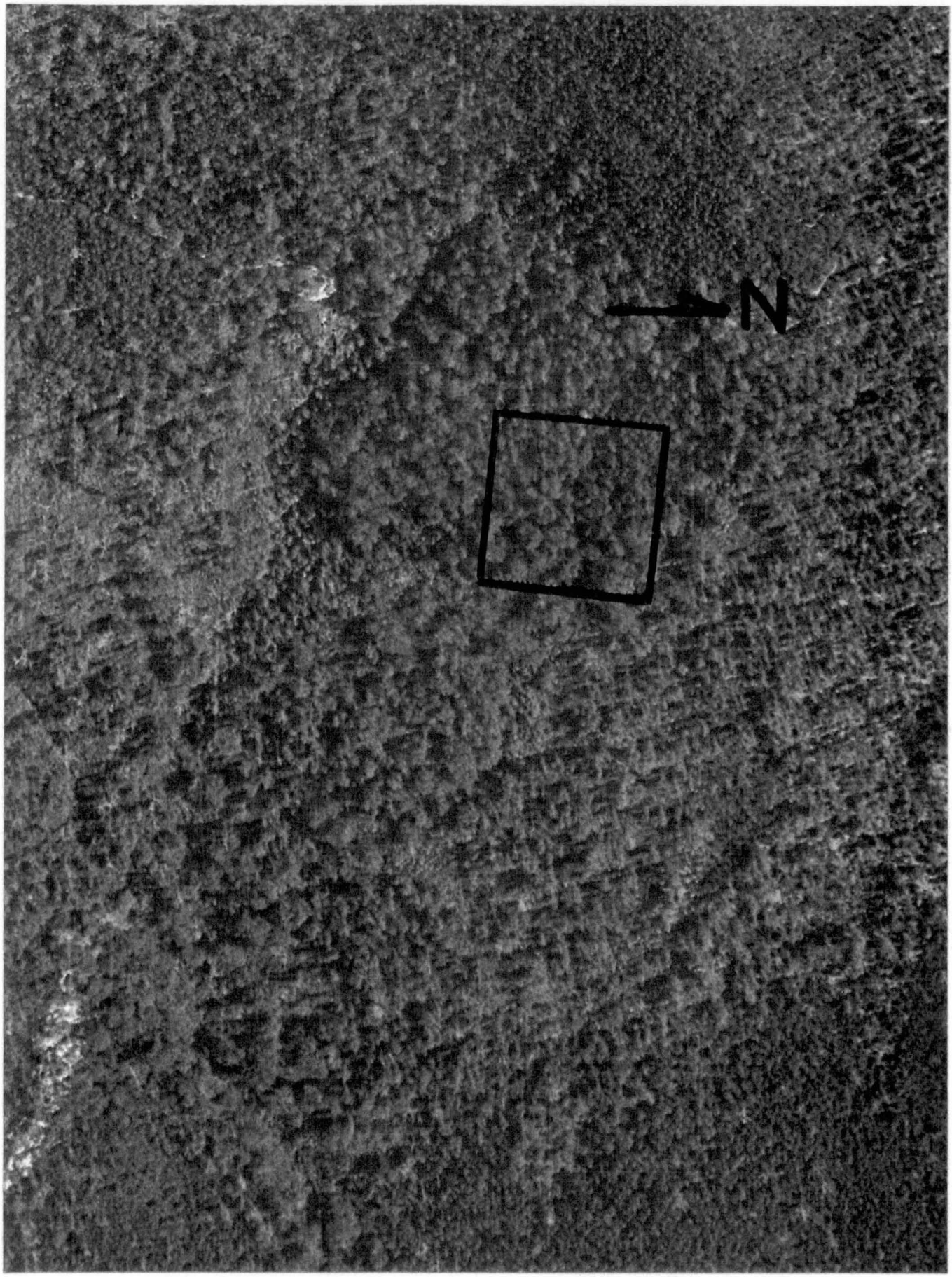


Figure 3.9a: The trapping area prior to the 1967 wildfire.

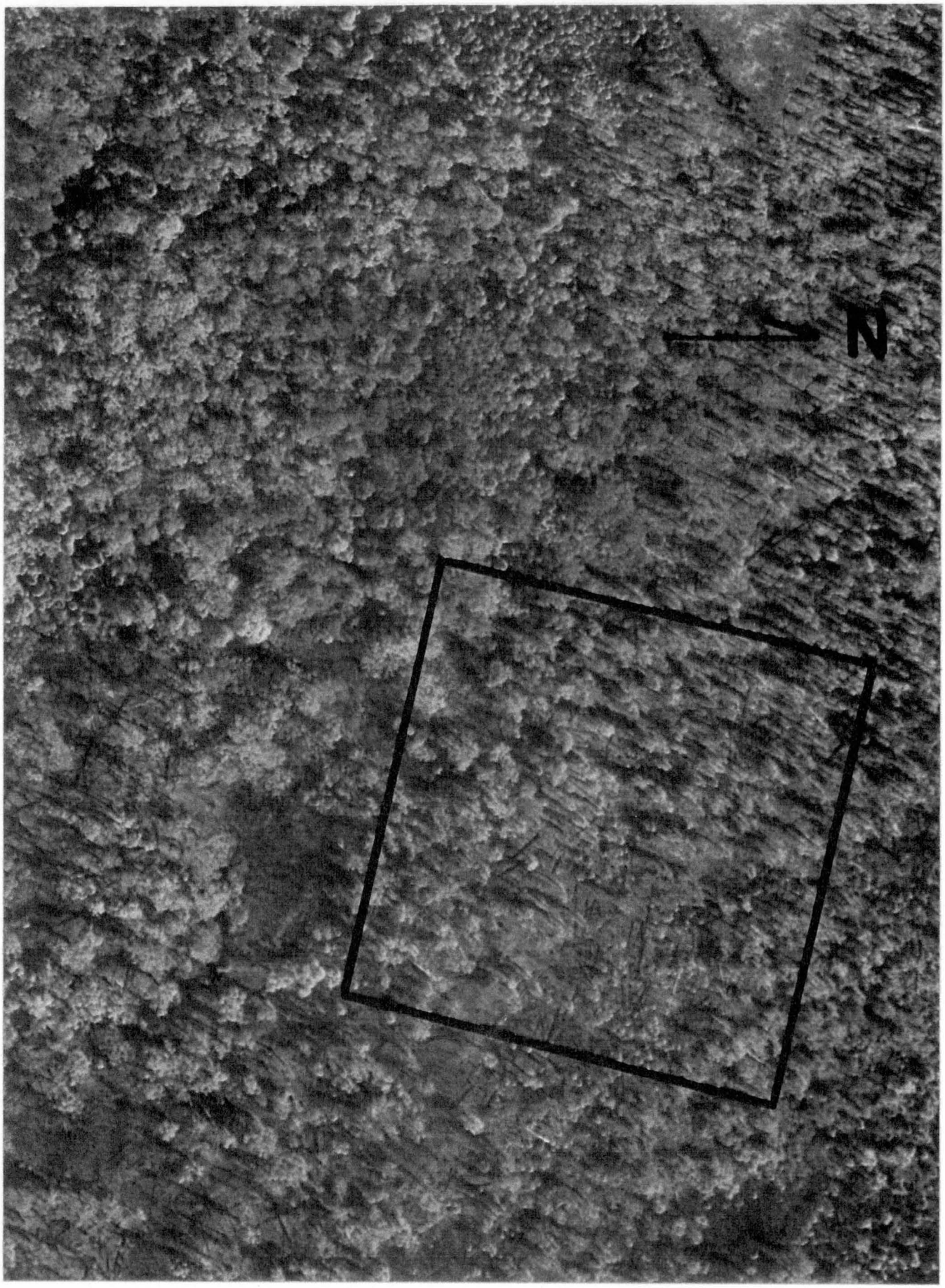


Figure 3.9b: The trapping area immediately after the 1967 wildfire.

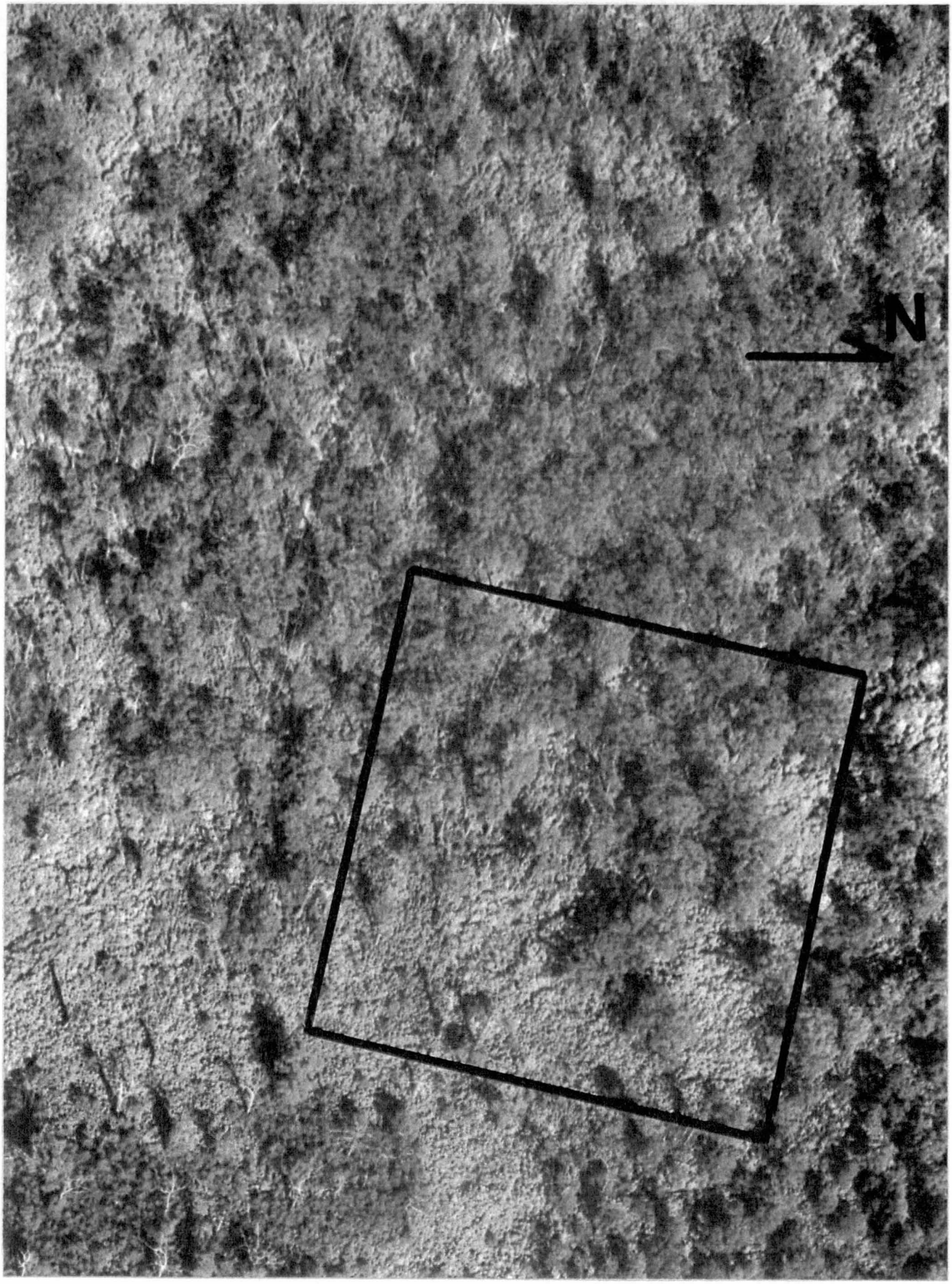


Figure 3.9c: The trapping area photographed in December 1988.

1b) were probably burned the least and have recovered most quickly. Habitat group 3, where soil moisture appears to be lowest may have been subjected to more intense burning and is recovering to a eucalypt dominated overstorey more slowly.

3.5 Summary

Variation in the floristics and structure of the vegetation over the trapping grid was classified and ordinated into four heterogeneous habitat groups. These groups were determined using multivariate statistical procedures and agree well with the subjective assessment of heterogeneity found before trapping.

It is probable that the 1967 bushfire is at least partly responsible for amplifying the variation seen in the vegetation today. It must be emphasized, however, that these habitat groups are not sharply discontinuous. Rather, they reflect different plant associations within a wet sclerophyll community at a particular point in time.

In the next chapter the habitat preferences of *R. l. velutinus* in wet sclerophyll forests are discussed with respect to the habitat groups described above.

CHAPTER FOUR
DIFFERENTIAL USE OF HABITAT BY *Rattus lutreolus velutinus*

4.1 Introduction

In Australia, the importance of floristic and structural variation has long been recognized in studies of small mammal habitat utilization. Although purely descriptive interpretations have been reported (e.g., Warneke 1971; Wainer 1976; Wainer and Gibson 1976) for the most part quantitative classifications of plant associations have been offered.

Some habitat assessments have involved univariate analyses to relate floristic or structural attributes to micro- or macrohabitats. Such analyses will detect irrelevant variables but may not take into account the effect of between-variable correlations (Dueser and Shugart 1978).

With the advent of readily available computer packages, many analyses now employ multivariate procedures. One such habitat classification procedure incorporated a polythetic, agglomerative, non-hierarchical clustering technique for classifying vegetation based on floristic data (Gullan 1978). It was successfully used as an indicator of preferred habitat for small mammals in a number of subsequent studies (e.g., Braithwaite *et al.* 1978; Stoddart and Braithwaite 1979; Gullan and Robinson 1980). The method of Gullan (1978) has been particularly useful in assessing food resource availability for a variety of ground-dwelling mammals (e.g., Watts and Braithwaite 1978; Braithwaite and Gullan 1978; Cockburn 1981a, 1981b).

The investigation of small mammal habitat preference using structural rather than floristic parameters has involved a much wider range of techniques. Visual estimates of vegetative cover at different heights using a modified Braun-Blanquet scale have been reported (e.g., Lunney *et al.* 1989). Subjective scores for cover at various heights have also been recorded (e.g., Newsome and Catling 1979; Braithwaite *et al.* 1984). Such scores have also been summed to give indices of structural complexity (e.g., Barnett *et al.* 1978; Murray 1980). Objective methods using portable sampling devices (e.g., Braithwaite and Gullan 1978; Braithwaite *et al.* 1978; Cockburn 1981a, 1981b; Hockings 1981; Driessen 1987); hemispherical photographic

techniques (Norton 1983); and light intensity measurements (Fox and Fox 1978; Fox 1979b) have all been used to correlate animal captures with structural features.

Few researchers have used multivariate methods to classify both the structural and floristic attributes of different habitats. Wilson *et al.* (1990) used a polythetic-agglomeration procedure (MACINF: Ross 1982) to classify both structural and floristic attributes of different habitat types at intervals after fire.

Today, polythetic-divisive classification procedures such as TWINSPAN (Hill 1979a: see Section 3.2.2) are generally favoured over agglomerative methods. Agglomerative clustering strategies start with individual samples which are successively combined into larger clusters until all data are contained in a single large group. Such methods are prone to picking up meaningless "noise" because they examine small distances between samples. This "noise", or stochastic variation, may distort subsequent clusters (Poore 1956; Gauch and Whittaker 1981).

TWINSPAN is now used routinely for identifying and classifying plant associations. It is increasingly being incorporated into animal studies as a means of revealing information about ecosystem components. Recent examples include the classification of freshwater invertebrate assemblages and the subsequent use of indicator species to predict stream acidity (Wade *et al.* 1989); the classification of reed marshes in relation to the habitat requirements of breeding bird communities (Anselin and Meire 1986); and small mammal habitat utilization in heterogeneous areas of high altitude grasslands (Fa *et al.* 1990).

Analysis of the capture data collected in this study reveal that individuals within the trappable population have an equal likelihood of capture (Section 2.6.3). To draw conclusions about the way in which these individuals were using their habitat, capture data were related directly to the four heterogeneous habitat groups described in Section 3.3. This procedure differs from some hypothesis-generating techniques described in the literature. In many studies where a multivariate analysis of habitat variables is used to investigate the habitat preferences of a particular species, the relative importance of each attribute is assessed using principal

components analysis. Hypotheses about habitat use are then generated by relating captures to the most important environmental parameters using, for example, multiple regression analysis (e.g., Cockburn 1981a; Chan 1990) or discriminant function analysis (Dueser and Shugart 1978, 1979; Morris 1984; Seagle 1985).

However, hypothesis-generating procedures were inappropriate for this study. Habitat heterogeneity has already been subjectively assessed prior to trapping and then tested using TWINSPAN (Hill 1979a) and DECORANA (Hill 1979b). This has yielded four separate habitat types within the wet sclerophyll community. The rate of capture within each group can, therefore, be assessed directly.

Because there was no significant difference in re-trappability between each sex or age class, total captures rather than the total number of individuals were used to indicate differential habitat use. It is not possible to determine what individuals were doing in a particular habitat group immediately prior to being trapped but capture rates within habitat groups can be compared and used to indicate the extent of differential habitat use within a heterogeneous environment.

4.2 Capture data

A total of 73 individuals were trapped 706 times throughout the study. The number of captures in each habitat group is shown in Table 4.1 and Figure 4.1. Chi-square analyses were conducted after the application of Yate's continuity correction (Sokal and Rohlf 1969) to determine whether it was more likely that one sex would be caught in a particular habitat type. The null hypothesis of equal likelihood was rejected at the 0.05 level of significance.

The number of male and female captures for the entire study did not differ significantly (342 male captures: 364 female captures; χ^2=0.625, d.f.=1, P>0.25). However, it is apparent from Table 4.2 that the rates of capture differed markedly both temporally and spatially. Overall, females were more likely to be captured in habitat group 1a (χ^2=8.11, d.f.=1, P<0.01) and habitat group 3 (χ^2=8.8, d.f.=1, P<0.01) than males, and males were more likely to be

Table 4.1: Number of captures in each heterogeneous habitat group (see text for an explanation of the number of captures per trap per 100 captures).

Habitat Group	No. of Captures Male	Female	Total	No. of trap points	No. of captures per trap per 100 capt.	Ratio of captures
1a	92	136	228	9	3.5882	11.06: 1
1b	150	133	283	39	1.0280	3.17: 1
2	84	56	140	28	0.7083	2.18: 1
3	16	39	55	24	0.3245	1.00: 1
TOTAL	**342**	**364**	**706**	**100**		

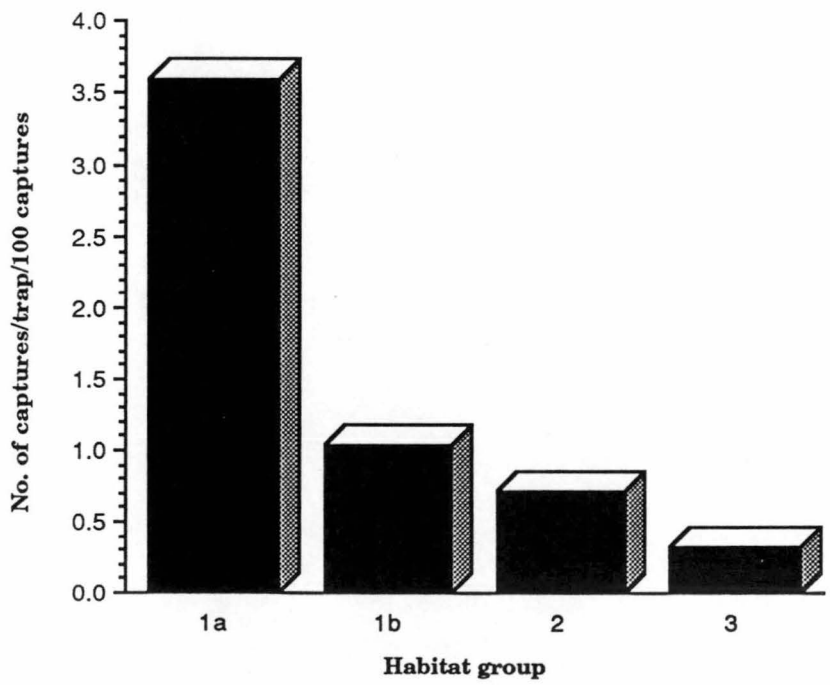


Figure 4.1: The number of captures in each habitat group expressed as number of captures per trap per 100 captures (see text for explanation).

trapped in habitat group 2 (χ^2=5.21, d.f.=1, P<0.05) than females. There was an equal likelihood of capture of either sex in habitat group 1b.

Capture rates also differed significantly within seasons in each habitat group. The rates for these seasons, namely: dispersal 1989; winter; breeding; and dispersal 1990 are summarized below:

- Habitat group 1a

Before the breeding season the female capture rate was significantly higher than the male capture rate (Table 4.2). At the onset of breeding the number of female captures declined and the number of males increased noticeably. Throughout the breeding season male captures were significantly higher than female captures (χ^2=10.01, d.f.=1, P<0.01).

- Habitat group 1b

There were equivalent numbers of captures of males and females prior to the breeding season. At the onset of breeding the number of female captures declined. Male capture rates remained constant but differed significantly from female capture rates (χ^2=7.27, d.f.=1, P<0.01).

- Habitat group 2

Capture rates during the dispersal and breeding seasons were equal. A trend towards more male captures was apparent during winter (χ^2=4.89, d.f.=1, P<0.05).

- Habitat group 3

Few captures were recorded in this habitat type. There were no male captures during the winter or the breeding season. During the 1989 dispersal season more male captures were recorded than female captures (χ^2=8.47, d.f.=1, P<0.01). However, the female capture rate was significantly higher than that of the males in the 1990 dispersal season (χ^2=7.69, d.f.=1, P<0.01).

To make between-group and between-season comparisons, the effect of having unequal numbers of trap stations in each habitat group was negated

Table 4.2: The number of captures of each sex for each group in each season.

Habitat Group	Season	Captures Males : Females			Total	χ^2 (d.f.=1)	Summary	P
	Dispersal 89	11	:	32	43	10.76	M<F	**
1a	Winter	8	:	63	71	41.07	M<F	***
	Breeding	57	:	27	84	10.01	M>F	**
	Dispersal 90	16	:	14	30	0.03	M=F	n.s.
		92	:	136	228	8.11	M<F	**
	Dispersal 89	24	:	20	44	0.20	M=F	n.s.
1b	Winter	52	:	61	113	0.57	M=F	n.s.
	Breeding	56	:	30	86	7.27	M>F	**
	Dispersal 90	18	:	22	40	0.225	M=F	n.s.
		150	:	133	283	0.905	M=F	n.s.
	Dispersal 89	16	:	13	29	0.14	M=F	n.s.
2	Winter	31	:	15	46	4.89	M>F	*
	Breeding	28	:	15	43	3.35	M=F	n.s.
	Dispersal 90	9	:	13	22	0.41	M=F	n.s.
		84	:	56	140	5.21	M>F	*
	Dispersal 89	15	:	2	17	8.47	M>F	**
3	Winter	0	:	21	21	19.05	M<F	***
	Breeding	0	:	4	4	n.a.	n.a.	n.a.
	Dispersal 90	1	:	12	13	7.69	M<F	**
		16	:	39	55	8.8	M>F	**
	Total	342	:	364	706	0.625	M=F	n.s.

* P<0.05
** P<0.01
*** P<0.001

Table 4.3: The seasonal distribution of captures of *R. l. velutinus* (March 1989 - 01 June 1990).

Season	Date	No. of trapping sessions	Captures/ trap/ 100 captures Habitat group				
			1a	1b	2	3	Total
Dispersal 1989	20.iii.89 - 05.v.89	3	0.6767	0.1598	0.1467	0.1003	1.0835
Winter 1989	29.v.89 - 20.x.89	6	1.1174	0.4105	0.2328	0.1239	1.8846
Breeding 1989/90	13.xi.89 - 06.iv.90	6	1.3220	0.3124	0.2175	0 0236	1.8755
Dispersal 1990	30.iv.90 - 01.v1.90	2	0.4721	0.1453	0.1113	0.0767	0.8054
	Total	17	3.5882	1.0280	0.7083	0.3245	5.6490

by reducing total captures for each group to the number of captures per trap site for each 100 captures. This was done by dividing the number of captures in each habitat group by the number of traps in that group and then multiplying by 0.141643 (i.e., 100 / 706 captures). Table 4.3 shows the number of captures/trap/100 captures for each habitat group in each season.

The number of trapping sessions was the same for the winter and breeding seasons (six sessions). However, the two dispersal seasons had only three and two sessions, respectively. Total capture data for these seasons therefore were doubled or trebled so that direct comparisons could be made between seasons. These data are presented in Figure 4.2 and Table 4.4. A comparison between each sex is offered in Figure 4.3 and Table 4.5.

4.3 Habitat utilization

It is apparent from these data that individuals within the trappable population of *R. l. velutinus* used heterogeneous areas of vegetation differentially. Capture rates varied noticeably between habitat groups, sexes and seasons.

A strong preference was shown by females for habitat group 1a throughout the study (Figure 4.3b). This was particularly evident during winter where the number of captures per trap per 100 captures was 4.5 times greater than the capture rate for group 1b; 13.1 times greater than group 2; and 7.6 times greater than habitat group 3 (see Table 4.5).

At the same time, male captures were spread evenly between habitat groups 1a, 1b and 2. No captures were recorded in Group 3 (Figure 4.3a).

At the onset of breeding there was a seven-fold increase in the male capture rate in habitat group 1a, while male capture rates tended to remain the same in the other groups (see Table 4.5).

Multiple regression analyses were used to determine which structural components, if any, were influencing the distribution of captures. The number of captures of each sex was correlated with the presence of rocks and logs and the seven vegetation height classes shown in Table 4.6. These structural variables had been estimated using a Braun-Blanquet scale (Mueller-Dombois and Ellenberg 1974). Before the statistical tests were applied, a mid-point was determined for each rating. This value was then

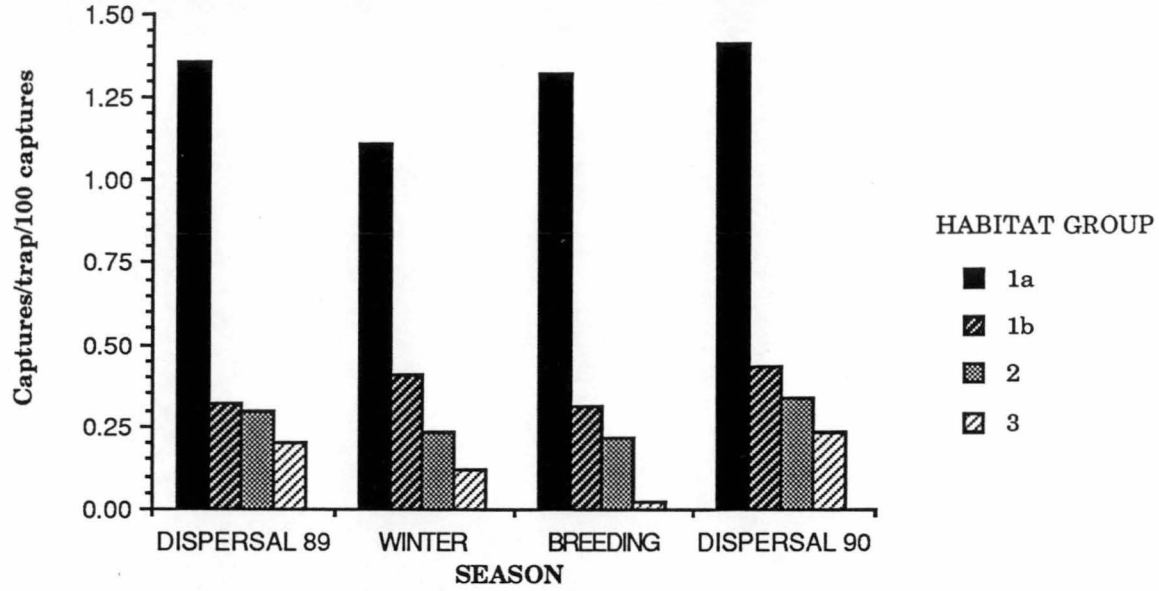


Figure 4.2: The rate of capture for each habitat group in each season (data are transformed to allow for different numbers of trapping sessions in each season - see text).

Table 4.4: Capture rates for each season after standardization of the two Dispersal seasons (see text for explanation of conversion factors).

Season	No. of trapping sessions	Conversion factor	No. of captures/ 100 captures			
			Habitat group			
			1a	1b	2	3
Dispersal 1989	3	x2	1.3534	0.3196	0.2934	0.2006
Winter 1989	6	x1	1.1174	0.4105	0.2328	0.1239
Breeding 1989/90	6	x1	1.3220	0.3124	0.2175	0.0236
Dispersal 1990	2	x3	1.4163	0.4359	0.3339	0.2301

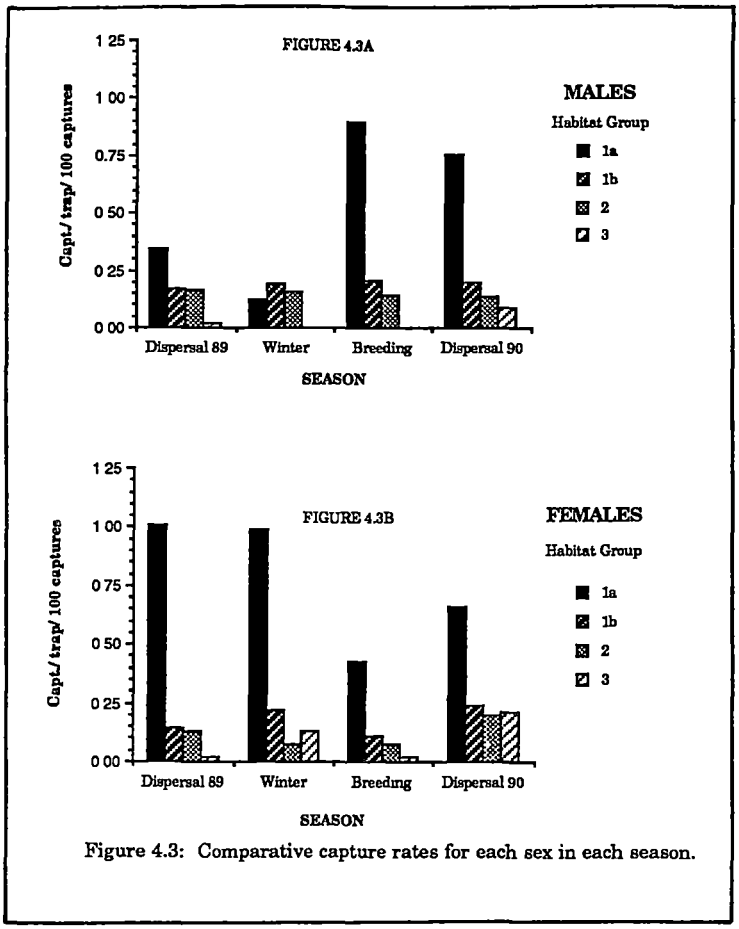


Figure 4.3: Comparative capture rates for each sex in each season.

Table 4.5: Transformed capture data for each sex in each season (M, males: F, females).

	No. captures/ trap/ 100 captures							
	Habitat Group							
	1a		1b		2		3	
Season	M	F	M	F	M	F	M	F
Dispersal 1989 (x2)	0.3462	1.0072	0.1742	0.1454	0.1618	0.1316	0.0177	0.0236
Winter 1989 (x1)	0.1259	0.9915	0.1889	0.2216	0.1569	0.0759	0.0000	0.1309
Breeding 1989/90 (x1)	0.8971	0.4249	0.2034	0.1090	0.1416	0.0759	0.0000	0.0236
Dispersal 1990 (x3)	0.7554	0.6609	0.1962	0.2397	0.1365	0.1974	0.0885	0.2124

Table 4.6: Habitat parameters used in correlating individual captures in each habitat group.

Braun-Blanquet Rating	Cover Estimate (%)	Mid-point	Arcsine √x (°)	Attribute (Cover)
0	0	0	0	0-20cm height
1	<1	0.5	4.05	21-50cm
2	1-5	3.0	9.97	51-100cm
3	6-25	15.5	23.18	1-2m
4	26-50	38.0	38.06	2-5m
5	51-75	63.0	52.54	5-10m
6	76-100	88.0	69.73	>10m
				Rocks
				Logs

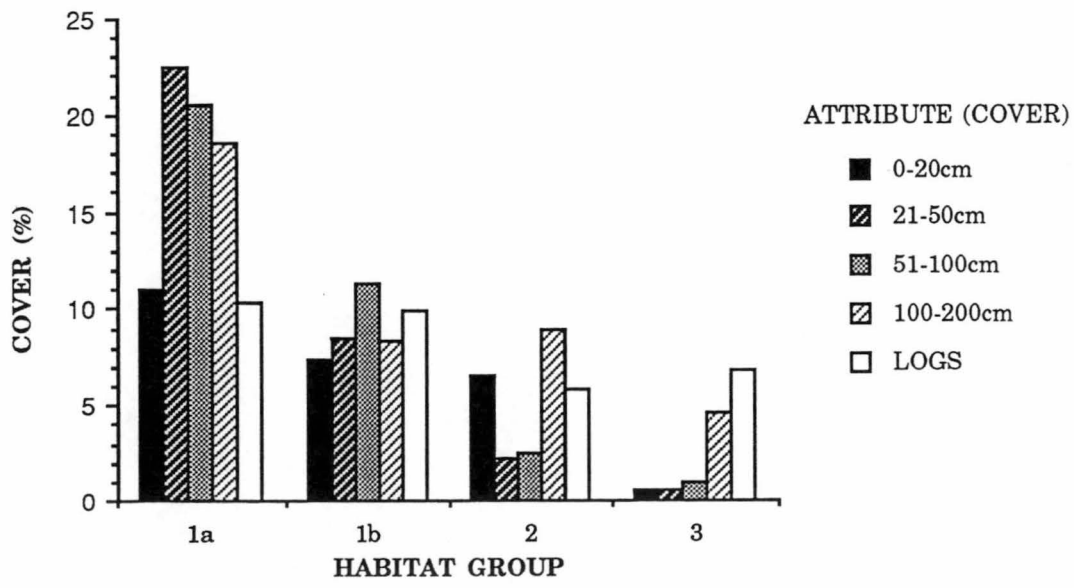


Figure 4.4: Mean values for cover attributes significantly associated with captures in each habitat group.

transformed using an arcsine $\sqrt{x}$ transformation.

Multiple regressions were performed using the Apple MacIntosh Statview SE+ program. A summary of these results is given in Table 4.7.

A clear preference for cover below one metre was apparent for each sex. Further regressions were carried out to determine whether a seasonal preference for particular cover attributes was evident. The results of these regressions are presented in Table 4.8.

A mean value for each cover attribute that was significantly associated with individual captures was calculated for each habitat group to determine the extent of each attribute in each group. These values are shown in Figure 4.4.

4.4 Discussion

The requirement for cover by forest populations of *R. l. velutinus* is well documented. Hocking (1975) recorded the percentage of organic ground cover to 30cm height within a two metre radius of each trap point. Chi-square ratio tests were applied to total captures to see if they were equivalent for each cover density rating. He found a significant preference for areas of densest cover, usually associated with the occurrence of *Blechnum wattsii.*

Murray (1980) scored numerous structural parameters, e.g., logs, ground cover, substrate and canopy cover and summed each to obtain a score of structural complexity in her study of habitat utilization by *Antechinus swainsonii, Pseudomys higginsi* and *R. l. velutinus.* She reported increased captures of *R. l. velutinus* in areas with greater than 50% ground cover and 50% canopy.

Driessen (1987) objectively quantified vegetation structure at various heights within one square metre of each trap using a portable sampling device and correlated each stratum with trapping success. He reported significant correlations between increased structural density below three metres and increased trapping success of *R. l. velutinus.*

In this study, *R. l. velutinus* within the trappable population showed significant preference for areas of the grid with high levels of cover below one metre. These areas best corresponded to habitat group 1a where dense stands of *B. wattsii* afforded almost total cover at this height. As the

amount of cover below one metre lessened, so did the capture rates for each sex.

What is of particular interest is that each sex has similar requirements for dense cover. The significantly higher female capture rate in areas of densest cover may indicate an exclusion of males from these areas. This matter will be discussed later.

Table 4.7: Beta coefficient tables from multiple regressions for each sex in all seasons. Bold type denotes P<0.05.

Table 4.7a: All male captures throughout the study

Attribute (Cover)	Coefficient	S.E.	Std. Coeff.	t-Value	P
Intercept	-1.23				
0-20cm	**0.139**	**0.035**	**0.383**	**4.028**	**0.0001**
21-50cm	0.019	0.042	0.049	0.439	0.6615
51-100cm	**0.128**	**0.036**	**0.349**	**3.574**	**0.0006**
1-2m	0.018	0.040	0.034	0.442	0.6593
2-5m	0.021	0.029	0.056	0.746	0.4575
5-10m	-0.029	0.018	-0.122	1.614	0.1100
>10m	0.041	0.024	0.119	1.678	0.0969
LOGS	**-0.066**	**0.025**	**-0.191**	**2.581**	**0.0115**
ROCKS	-0.040	0.044	-0.063	0.922	0.3589

Table 4.7b: All female captures throughout the study

Attribute (Cover)	Coefficient	S.E.	Std. Coeff.	t-Value	P
Intercept	-4.025				
0-20cm	0.038	0.064	0.067	0.599	0.5508
21-50cm	**0.199**	**0.078**	**0.331**	**2.540**	**0.0128**
51-100cm	0.115	0.066	0.200	1.737	0.0857
1-2m	0.133	0.074	0.162	1.802	0.0749
2-5m	-0.016	0.053	-0.026	0.296	0.7680
5-10m	-0.035	0.033	-0.097	1.082	0.2822
>10m	**0.104**	**0.045**	**0.191**	**2.289**	**0.0244**
LOGS	-0.076	0.047	-0.142	1.628	0.1070
ROCKS	-0.021	0.081	-0.021	0.264	0.7926

Table 4.8: Beta coefficient tables from multiple regressions for each sex in each season. Bold type denotes P<0.05.

Table 4.8a: Male captures - Dispersal 1989

Attribute (Cover)	Coefficient	S.E.	Std. Coeff.	t-Value	P
Intercept	-0.07				
0-20cm	**0.036**	**0.012**	**0.402**	**2.933**	**0.0043**
21-50cm	-0.011	0.015	-0.115	0.720	0.4733
51-100cm	0.010	0.013	0.110	0.784	0.4354
1-2m	-0.016	0.014	-0.123	1.124	0.2639
2-5m	0.007	0.010	0.071	0.656	0.5137
5-10m	-0.001	0.006	-0.025	0.228	0.8204
>10m	0.002	0.009	0.019	0.183	0.8550
LOGS	-0.003	0.009	-0.030	0.285	0.7761
ROCKS	0.021	0.016	0.134	1.361	0.1768

Table 4.8b: Female captures - Dispersal 1989

Attribute (Cover)	Coefficient	S.E.	Std. Coeff.	t-Value	P
Intercept	-1.482				
0-20cm	0.016	0.014	0.136	1.194	0.2356
21-50cm	**0.034**	**0.017**	**0.266**	**2.003**	**0.0482**
51-100cm	0.016	0.014	0.135	1.148	0.2541
1-2m	**0.039**	**0.016**	**0.222**	**2.430**	**0.0171**
2-5m	-0.001	0.012	-0.010	0.107	0.9153
5-10m	-0.001	0.007	-0.013	0.140	0.8889
>10m	**0.031**	**0.010**	**0.271**	**3.197**	**0.0019**
LOGS	-0.017	0.010	-0.150	1.687	0.0952
ROCKS	-0.004	0.018	-0.020	0.250	0.8035

Table 4.8 cont.: Beta coefficient tables from multiple regressions for each sex in each season. Bold type denotes P<0.05.

Table 4.8c: Male captures - Winter 1989

Attribute (Cover)	Coefficient	S.E.	Std. Coeff.	t-Value	P
Intercept	0.261				
0-20cm	**0.067**	**0.017**	**0.486**	**3.856**	**0.0002**
21-50cm	-0.011	0.021	-0.079	0.539	0.5911
51-100cm	0.150	0.018	0.107	0.826	0.4111
1-2m	-0.022	0.020	-0.108	1.071	0.2868
2-5m	0.013	0.014	0.088	0.882	0.3801
5-10m	0.001	0.009	0.016	0.156	0.8761
>10m	-0.005	0.012	-0.036	0.390	0.6977
LOGS	-0.012	0.013	-0.090	0.920	0.3598
ROCKS	0.043	0.022	-0.174	1.926	0.0572

Table 4.8d: Female captures - Winter 1989

Attribute (Cover)	Coefficient	S.E.	Std. Coeff.	t-Value	P
Intercept	-2.085				
0-20cm	-0.012	0.037	-0.037	0.318	0.7514
21-50cm	**0.118**	**0.045**	**0.356**	**2.608**	**0.0107**
51-100cm	0.060	0.038	0.190	1.581	0.1174
1-2m	**0.086**	**0.043**	**0.191**	**2.032**	**0.0451**
2-5m	-0.006	0.031	-0.017	0.188	0.8514
5-10m	-0.022	0.019	-0.111	1.192	0.2363
>10m	0.049	0.026	0.164	1.875	0.0640
LOGS	-0.044	0.027	-0.147	1.608	0.1113
ROCKS	-0.027	0.047	-0.048	0.573	0.5683

Table 4.8 cont.: Beta coefficient tables from multiple regressions for each sex in each season. Bold type denotes P<0.05.

Table 4.8e: Male captures - Breeding 1989 / 1990

Attribute (Cover)	Coefficient	S.E.	Std. Coeff.	t-Value	P
Intercept	-1.094				
0-20cm	0.033	0.024	0.153	1.382	0.1705
21-50cm	0.033	0.029	0.144	1.123	0.2643
51-100cm	**0.066**	**0.025**	**0.308**	**2.712**	**0.0080**
1-2m	0.033	0.027	0.106	1.204	0.2319
2-5m	0.013	0.020	0.057	0.650	0.5174
5-10m	-0.019	0.012	-0.135	1.534	0.1286
>10m	0.028	0.017	0.137	1.663	0.0998
LOGS	**-0.043**	**0.017**	**-0.213**	**2.475**	**0.0152**
ROCKS	-0.023	0.030	-0.061	0.764	0.4469

Table 4.8f: Female captures - Breeding 1989 / 1990

Attribute (Cover)	Coefficient	S.E.	Std. Coeff.	t-Value	P
Intercept	-0.365				
0-20cm	-0.010	0.015	0.082	0.679	0.4989
21-50cm	0.023	0.019	0.170	1.207	0.2305
51-100cm	**0.044**	**0.016**	**0.343**	**2.756**	**0.0071**
1-2m	-0.002	0.018	0.191	0.092	0.9273
2-5m	3.816E-5	0.013	-0.009	0.003	0.9976
5-10m	-0.009	0.008	2.841E-4	1.153	0.2520
>10m	0.022	0.011	-0.111	1.967	0.0523
LOGS	-0.014	0.011	-0.177	1.241	0.2180
ROCKS	-0.001	0.020	-0.004	0.046	0.9638

Table 4.8 cont.: Beta coefficient tables from multiple regressions for each sex in each season. Bold type denotes P<0.05.

Table 4.8g: Male captures - Dispersal 1990

Attribute (Cover)	Coefficient	S.E.	Std. Coeff.	t-Value	P
Intercept	-0.328				
0-20cm	0.004	0.010	0.040	0.351	0.7265
21-50cm	0.008	0.012	0.089	0.670	0.5044
51-100cm	**0.037**	**0.010**	**0.414**	**3.509**	**0.0007**
1-2m	0.022	0.012	0.175	1.902	0.0604
2-5m	-0.011	0.008	-0.117	1.289	0.2008
5-10m	-0.010	0.005	-0.176	1.924	0.0575
>10m	**0.016**	**0.007**	**0.196**	**2.295**	**0.0241**
LOGS	-0.008	0.007	-0.098	1.097	0.2754
ROCKS	-0.004	0.013	0.025	0.306	0.7599

Table 4.8h: Female captures - Dispersal 1990

Attribute (Cover)	Coefficient	S.E.	Std. Coeff.	t-Value	P
Intercept	-0.090				
0-20cm	0.019	0.014	0.192	1.356	0.1786
21-50cm	0.022	0.017	0.212	1.287	0.2013
51-100cm	-0.010	0.014	-0.103	0.705	0.4829
1-2m	0.004	0.016	0.025	0.221	0.8253
2-5m	-0.011	0.012	-0.105	0.936	0.3517
5-10m	0.001	0.007	0.010	0.089	0.9290
>10m	-0.002	0.010	-0.017	0.163	0.8706
LOGS	0.002	0.010	0.026	0.232	0.8167
ROCKS	0.024	0.018	0.136	1.337	0.1847

CHAPTER FIVE
ECOPHYSIOLOGY

5.1 Introduction

In addition to the investigation of demographic processes, this study included an analysis of the condition of individuals in the trappable population. Physical well-being is often related to ecological performance (Humphreys *et al.* 1984) and it was of considerable interest to determine whether individuals active in heterogeneous vegetation types differed in their ability to cope with environmental stressors. Lidicker (1978) emphasized the importance of an integrated approach to the study of natural populations when he stated "...one cannot ignore an organism's physiology and expect to fully understand its population dynamics."

The interactions of demographic and physiological processes of some small mammals in temperate and boreal regions of the northern hemisphere have been well-studied, especially in the context of population regulation in some microtine rodent species (see Krebs and Myers 1974; Christian 1980 for reviews).

In Australia, many ecophysiological investigations have reported on the life histories of several species of dasyurid marsupials which display unusual post-mating male mortality (see Lee and McDonald 1985 for a comprehensive review).

The ecophysiology of Australian native rodents has been less well studied. Aspects of the physiology and population ecology of the Australian bush rat, *Rattus fuscipes* (e.g., Robinson 1975, 1987; Barnett 1977; Stewart and Barnett 1983; McDonald *et al.* 1988), the mosaic-tailed rat, *Melomys* sp. (Kemper *et al.* 1987) and the common rock rat, *Zyzomys argurus* (Bradley *et al.* 1988) have been reported but there have been no studies which have detailed aspects of the ecophysiology of *R. lutreolus.*

There is no general agreement about the best way in which to assess physical 'condition' although many morpho-physiological indices have been proposed (see Shvarts 1975 and Humphreys *et al.* 1984 for reviews). The essence of a morpho-physiological approach is that an estimation of a

number of indices from representative individuals can lead to an assessment not only of individual fitness but also of community performance.

In this study, blood constituents were used to monitor seasonal changes in individuals in the trappable population. Additionally, stress responses were monitored by measuring plasma corticosterone levels as an indicator of adrenal function. An elevation in corticosterone leads to immunosuppression and so the monitoring of such an index can provide valuable information about both stress and disease.

These physiological indices were combined with information gathered throughout the study on tail-wounding and excessive ectoparasite burdens to determine whether differences existed in the morpho-physiological profiles of individuals active in 'preferred' and 'peripheral' habitat.

5.2. Methods

5.2.1 Blood sampling

At first capture in each trapping session, blood samples not exceeding 500µl, or 5% of total blood volume, were collected from each individual. Samples were obtained by infra-orbital sinus puncture (Riley 1960) within two minutes of finding an animal in a trap. Although this technique may be applied safely without anaesthesia (*ad hoc* Committee on Acceptable Field Methods in Mammalogy 1987), anaesthetic grade diethyl ether was used to minimize distress.

Blood was run through a heparinized 75µl microhaematocrit tube and collected in a 1.5ml polypropylene microfuge tube containing a small amount of lithium heparinate (Sigma Diagnostics, St. Louis, U.S.A.). Samples were kept cold until sub-samples could be taken for the measurement of haematological parameters.

5.2.2 Problems associated with blood sampling

There are many problems associated with the accurate assessment of parameters from blood collected from free-living individuals. It is reasonable to suspect that the length of time that an individual spends in a trap prior to handling may induce changes in the measured variables. The diurnal secretion pattern of some blood metabolites combined with the

interrelationships of physiological systems may also contribute to sample variations beyond actual population variation.

It has been reported recently that blood collection from the infra-orbital sinus affects recapture rates and survivorship in prairie voles, *Microtus ochrogaster* (Frase *et al.* 1990). However in this study, there was no evidence of cumulative damage or infection from the four-weekly blood sampling regime. As mentioned, many individual *R. l. velutinus* were trapped repeatedly during the study and appeared unaffected by the constant handling, anaesthesia and blood collection.

Prior to a blood sample being collected, each trapped individual is subjected to nutritional and spatial restrictions by virtue of its empoundment in a trap. These restrictions contribute to capture stress and a concomitant increase in plasma corticosterone levels (Fiennes 1982). Accurate measurement of 'resting' glucocorticoid values have been found to be subject to sampling errors exacerbated by capture and immobilization techniques in many species (e.g., Alaskan moose, *Alces alces* Franzmann *et al.* 1975; and bighorn sheep, *Ovis canadensis* MacArthur *et al.* 1986; Harlow *et al.* 1987). Further, Cook *et al.* (1973) reported that, in laboratory rats, the inhalation of ether vapour for 30 seconds was sufficient to cause the immediate release of ACTH into the blood stream and that maximal adrenal corticosterone release was apparent within 2.5 minutes.

The extent of psychological perturbation must also be considered. Emotional stressors initiate a stress response as effectively as an aversive physical stimulus (e.g., tape-recorded wolf howls played to captive deer fawns: Moen *et al.* 1978). In addition, it is also known that susceptibility to capture stress varies between stressors (Shepherd 1981) and that genotypic variations within individual species influences the extent of a pituitary-adrenal response (Dantzer and Mormede 1983).

Clearly, the influence of trap-mediated pituitary-adrenal responses must be taken into account when interpreting data obtained from blood samples. In many studies efforts have been made to reduce the effects procedures such as trapping and handling have on blood parameters. Some researchers have brought animals to the laboratory for an acclimation period prior to bleeding (e.g., Barnett 1973; Robinson 1975; Cheal *et al.*

1976). This has usually involved holding individuals for several days and was inappropriate in this study where minimal disruption was desired. Instead, every effort was made to minimize the restrictions which individuals experienced while trapped. Nesting material was added to each trap which was, in turn, placed in a plastic bag. This reduced the chances of individuals having 'artificial' haematological values, such as elevated haematocrit due to cold (Maclean and Lee 1973) or heat and dehydration (Guyton 1971). Traps were emptied starting at first light each morning to reduce the amount of time individuals spent in traps.

The effect of ether on circulating levels of corticosterone could not be minimized. Ether vapour was administered for one minute to ensure that each animal was sufficiently anaesthetized and this may have caused increased levels of corticosterone (Cook *et al.* 1973). To circumvent this problem, the consequences of capture, handling and anaesthesia were viewed as an acute stressor (*sensu* Selye 1936). The ability of each individual to respond to the imposition of such a stressor was then measured by comparing not only total corticosterone concentrations but also the partitioning of the steroid into biologically active and inactive components. Corticosteroids circulating in plasma are mostly bound with high affinity to corticosteroid binding globulin (CBG) and albumin and are therefore rendered inactive (Bradley *et al.* 1976). It is the concentration of free, biologically active hormone that is relevant to the various disease states that may manifest themselves given a persistent state of stress (Tait 1982).

By partitioning the corticosterone concentration into these components, an indication of the response to acute (i.e., capture and handling) stress can be gained and compared for individuals active in different habitat groups at different times of the year.

5.2.3 Haematological methods

An erythrocyte count was made after diluting a 10µl blood sample 1:200 in Hayem's solution (see Appendix 6 for the preparation of each solution). Leucocytes were counted after diluting 10µl of blood 1:100 in Turk's solution. Each suspension was counted in a haemocytometer with an improved Neubauer ruling. A thin methanol-fixed blood smear stained with Wright's

stain was used to determine counts of lymphocytes and neutrophils.

The haemoglobin concentration was measured by the cyanomethaemoglobin procedure. 10µl of blood was added to 2.0ml of Drabkin's solution (Drabkin 1949) and the optical density was measured at 540nm using a spectrophotometer (Beckman model 26). A standard haemoglobin solution (Sigma Diagnostics, St. Louis, U.S.A.) was also diluted in Drabkin's solution to relate optical density to haemoglobin concentration.

Haematocrit and total plasma protein concentrations were obtained after drawing up a small amount of whole blood into a 75µl microhaematocrit tube and centrifuging for four minutes at 10 000rpm. Total plasma protein concentration was determined using a portable clinical refractometer (Atago SPR-N, Ogowa Seiki, Japan).

Plasma albumin concentration was determined spectrophotometrically after the method of Rodkey (1965). The absorbance of known concentrations of a standard (rat albumin Fraction V: Sigma Diagnostics, St. Louis, U.S.A.) and *R. l. velutinus* plasma albumin was measured at 615nm after first mixing with bromocresol green reagent.

Mean corpuscular haemoglobin concentration (MCHC), mean corpuscular haemoglobin (MCH) and mean corpuscular volume (MCV) were derived in the following way:

$$\text{MCHC} = 100 \times \frac{\text{haemoglobin concentration (g/dl)}}{\text{haematocrit}}$$

$$\text{MCH} = 10 \times \frac{\text{haemoglobin concentration (g/dl)}}{\text{erythrocyte count } (10^{-12}\text{xcells/l})}$$

$$\text{MCV} = 10 \times \frac{\text{haematocrit (\%)}}{\text{erythrocyte count } (10^{-12}\text{xcells/l})}$$

5.2.4 Plasma corticosterone assays

- isotopes and chemicals

[1,2,6,7-^{3}H]-corticosterone with a specific activity of 94Ci.mmol^{-1} (Radiochemical Centre, Amersham, England) and non-radioactive steroid

(Sigma Diagnostics, St. Louis, U.S.A.) were donated by Dr. A. J. Bradley. All other reagents (analytical grade) were purchased from local commercial sources.

- steroid-protein interactions

Free, CBG-bound and albumin-bound corticosterone in *R. l. velutinus* plasma were calculated by the method of Tait and Burstein (1964). A high-affinity binding constant of 3.0×10^7 and a low-affinity corticosterone-albumin bound constant of 1.85, already derived for *Rattus* sp. by Westphal (1971), were used.

- radioimmunoassay protocols

Plasma total corticosteroid concentration was measured using a competitive protein-binding assay (after Murphy *et al.* 1963). The binding solution contained 0.5% radioactively-labelled corticosterone (BH^3: $10\mu Ci.ml^{-1}$); 2.0% dog plasma from which endogenous steroid had been stripped using column chromatography (Sephadex G-50 in 0.05M phosphate buffer, pH 7.7 at 45°C: Bassett and Hinks 1969); and 0.0625% normal human γ-immunoglobulin (Commonwealth Serum Laboratories, Melbourne, Australia) in a 0.05M phosphate buffer, pH 7.4.

- extraction of plasma steroids

25µl plasma samples were mixed thoroughly in 1.0ml of absolute ethanol to extract the steroid. The extraction efficiency for corticosterone was calculated, using a known dose and stripped dog plasma, at between 98 - 100% (n=10). Samples were centrifuged at 2500rpm for 10 minutes and a 25µl aliquot of the supernatant (ethanol + steroid) was taken for radioimmunoassay (RIA).

- measurement of total corticosterone

The 25µl aliquots were air-dried in glass test-tubes until all ethanol had evaporated. 0.5ml of binding solution was then added and each tube was incubated at 35°C for five minutes. This period was sufficient to disassociate bound BH^3 from the binding protein. Each sample was vortexed for one

minute and incubated overnight at 4°C.

Duplicate standards containing 0-3200pg corticosterone in 50µl ethanol were treated similarly.

Following incubation, 0.5ml dextran-coated charcoal (DCC: see Appendix 6) was added to each sample for 15 minutes at 4°C. The DCC acts to bind all unbound BH^3 and plasma corticosterone still in solution. Centrifuging settles the DCC-bound steroid leaving only protein-bound corticosterone in the supernatant. 150µl of the supernatant was added to 2.0ml of scintillation fluid (Ecoscint, National Diagnostics, Somerville, U.S.A.) and counted using a Beckman LS 5801 liquid scintillation spectrometer with automatic quench correction. Assay results were computed automatically using an RIA program.

- measurement of MCBC

Plasma high-affinity corticosteroid binding capacity (MCBC) was used to estimate CBG and was measured by the DCC-separation method of McDonald *et al.* (1981). 50µl of absolute ethanol containing $5\mu Ci.ml^{-1}$ BH^3 and $10ng.\mu l^{-1}$ corticosterone was air-dried in glass test-tubes. A 25µl aliquot of *R. l. velutinus* plasma was added to each tube and vortexed thoroughly. Each tube was then centrifuged at 2500rpm for 10 minutes to settle the plasma and incubated overnight at 4°C. 0.5ml of DCC was added and the same assay procedure as described for total corticosterone (above) was followed.

Non-specific binding was calculated by adding 25µl of distilled water to tubes containing added steroid and assaying as above.

The established specific activity of the added steroid plus the measured endogenous steroid were used to calculate the MCBC for each sample.

5.2.5 The effect of ether on plasma corticosterone concentration

To quantify the effects of ether stress on *R. l. velutinus,* a separate field experiment was conducted. Six males and nine females were trapped between 18 July and 13 August 1989 in wet sclerophyll habitat similar to that found on the trapping grid. Each was anaesthetized for 60 seconds and held in a calico bag for 10 minutes. They were then given a further anaesthetic ether dose (60 seconds) and bled from the infra-orbital sinus. The 10 minute delay before bleeding was to ensure that maximal adrenal release of corticosterone had occurred (Cook *et al.* 1973). Haematological and corticosterone parameters were calculated in the same way as described previously, and are presented in Section 5.3.3.

5.3 Results

A physiological profile is presented for males and females born in the 1988/ 1989 breeding season. Comparisons are made between sexes for each trapping session using unpaired Student's t-tests. If few differences occur between males and females, data can be grouped and the effects of habitat on condition can be compared (see Section 5.3.5).

Sample sizes were always small due to the low densities of individuals in the trappable population and between sample variation for some blood parameters was high. Consequently, H_0 was only rejected when $P<0.01$.

Few data were obtained for many blood parameters from adults born before 1989 or from individuals born in 1990 and between sex comparisons for each of these age classes are not presented. The data that were collected are presented in Appendix 7.

5.3.1 Haematology

- *total proteins* (Table 5.1)

The mean total plasma protein concentration in males remained stable throughout winter before falling during the breeding season. In the females, the mean total plasma protein concentration rose gradually through the winter and into the breeding season before falling slightly at the end of the study. No significant differences were detected between sexes at any time (see Appendix 5.1).

Table 5.1: Changes in the plasma proteins of individuals born in 1989. (Values are means ± 1 SD, with the number of individuals in parentheses).

		MALES		FEMALES	
TRAPPING SESSION	**DATE**	**TOTAL PROTEIN (g/dl)**	**PLASMA ALBUMIN (g/dl)**	**TOTAL PROTEIN (g/dl)**	**PLASMA ALBUMIN (g/dl)**
	Dispersal				
3	1.v.89	7.4±0.8 (6)	4.0±0.4 (6)	6.2±1.0 (4)	2.4±1.5 (4)
	Winter				
4	29.v.89	7.4±0.4 (4)	3.2±1.4 (4)	6.5±0.6 (4)	3.2±1.1 (4)
5	26.vi.89	7.3±1.1 (3)	5.2±0.6 (3)	6.7±0.5 (5)	4.2±0.9 (5)
6	24.vii.89	7.4±0.6 (4)	4.5±0.6 (4)**	7.0±0.5 (5)	3.3±0.4 (5)**
7	21.viii.89	7.3±0.6 (3)	4.3±0.6 (3)	6.9±0.6 (5)	3.8±1.1 (5)
8	18.ix.89	7.4±0.4 (3)	4.4±0.7 (3)	7.0±0.3 (6)	4.0±0.8 (6)
9	16.x.89	7.1±0.4 (5)	5.0±0.8 (5)	6.7±0.8 (7)	4.0±0.8 (7)
	Breeding				
10	13.xi.89	7.2±0.6 (11)	4.4±0.6 (11)	7.2±0.7 (8)	3.8±0.6 (8)
11	11.xii.89	7.0±0.5 (13)	4.2±0.6 (13)	7.3±0.5 (7)	4.0±0.8 (7)
12	8.i.90	6.9±0.5 (8)	3.7±0.7 (8)	7.4±0.6 (5)	3.6±0.4 (5)
13	5.ii.90	7.1±0.4 (6)	3.3±0.4 (6)	6.7±1.3 (5)	2.6±0.9 (4)
14	5.iii.90	7.1±0.4 (5)	3.0±0.4 (5)	6.8±0.7 (3)	2.8±1.0 (3)
15	2.iv.90	6.9±0.4 (3)	-	7.2 - 8.0 (2)	2.3 - 4.0 (2)
	Dispersal				
16	30.iv.90	7.2±0.0 (3)	3.4±0.1 (3)	7.2±0.7 (4)	3.4±1.0 (4)
17	28.v.90	7.4 - 7.8 (2)	3.3 - 3.4 (2)	6.4	2.2

** $P<0.01$ see text for discussion.

- *plasma albumin* (Table 5.1)

Mean plasma albumin concentrations for both sexes rose gradually until the middle of the breeding season. At this time, concentrations declined until they approached similar values to those recorded at the beginning of the study. No significant differences were detected between sexes except in late July 1989 when mean female albumin concentration exceeded male albumin concentration ($t=3.896$, d.f.=7, $P<0.01$: Appendix 5.1).

- *erythrocyte parameters* (Table 5.2)

Mean values for all erythrocyte variables showed changes with time of the year. There were no significant differences recorded between the sexes for haematocrit, haemoglobin, red cell count, MCH or MCV. At the onset of the breeding season (Session 10) MCHC concentrations were lower in males than in females ($t=3.062$, d.f.=17, $P<0.01$: Appendix 5.2).

- *leucocyte parameters* (Table 5.3)

The mean leucocyte count showed irregular changes in both sexes but did not differ significantly at any time (see Appendix 5.3). In the males, a gradual increase was evident through the winter and into the breeding season. A sharp increase was evident from sessions 13 to 16. There were irregular fluctuations in the lymphocyte: neutrophil ratio in the males. The lymphocyte: neutrophil ratio was more constant for females.

5.3.2 Plasma corticosterone concentration

- *total corticosterone*

The plasma total corticosterone concentration of male and female *R. l. velutinus* born in 1989 were compared. Levels for each sex fluctuated in the range 6.1±1.2μM (n=3) - 9.9±4.6μM (n=5) during the winter trapping sessions (see Table 5.4). During the breeding season, male values declined to range from 3.6±1.4μM (n=8) to 5.7±2.9μM (n=5). At the same time, female total corticosterone concentration increased to range from 7.8±4.5μM (n=4) to 13.2±2.6μM (n=7). These values were not sustained and by the end of the study mean values for each sex had returned to levels similar to those

Table 5.2a: Changes in the erythrocyte indices of males born in 1989 (Values are means ± 1 SD, with number of individuals in parentheses).

TRAPPING SESSION	DATE	HAEMATOCRIT (%)	HAEMAGLOBIN ($g.dl^{-1}$)	10^{12}x RED BLOOD CELLS ($cells.L^{-1}$)	MCHC ($g.dl^{-1}$ red cells)	MCH (pg)	MCV (fl)
	Dispersal						
3	1.v.89	44.2±2.7 (6)	19.1±1.5 (6)	-	43.3±3.2 (6)	-	-
	Winter						
4	29.v.89	51.1±4.0 (4)	16.2±1.2 (4)	-	31.8±1.3 (4)	-	-
5	26.vi.89	48.0±1.9 (3)	18.9±2.0 (3)	7.1±1.8 (3)	39.3±2.6 (3)	27.0±5.3 (3)	69.9±16.4 (3)
6	24.vii.89	48.6±2.8 (4)	18.6±0.7 (4)	6.2±0.5 (4)	38.3±1.0 (4)	30.4±3.6 (4)	79.7±11.4 (4)
7	21.viii.89	47.3±1.1 (3)	18.7±1.0 (3)	8.6±2.2 (3)	39.5±1.9 (3)	22.9±6.9 (3)	57.5±15.3 (3)
8	18.ix.89	46.0±2.6 (3)	17.2±1.5 (3)	7.8±1.8 (3)	37.5±2.8 (3)	22.7±5.9 (3)	60.8±15.4 (3)
9	16.x.89	49.6±5.5 (6)	17.8±2.1 (6)	7.2±0.7 (6)	35.8±0.7 (6)	24.8±3.1 (6)	69.3±7.8 (6)
	Breeding						
10	13.xi.89	47.3±2.4 (11)	16.9±1.2 (11)	7.0±1.5 (11)	35.6±1.2 (11)**	24.6±4.1 (11)	69.2±11.1 (11)
11	11.xii.89	47.8±2.2 (13)	17.4±0.9 (13)	7.4±1.2 (13)	36.5±0.9 (13)	24.1±3.0 (13)	66.0±7.7 (13)
12	8.i.90	44.8±6.4 (8)	15.7±2.6 (8)	7.2±2.0 (8)	35.2±3.4 (8)	23.1±7.2 (8)	64.7±14.7 (8)
13	5.ii.90	44.6±4.9 (6)	15.5±1.8 (6)	6.5±0.8 (6)	34.8±2.6 (6)	24.0±2.4 (6)	69.6±10.3 (6)
14	5.iii.90	41.1±6.9 (5)	14.9±2.1 (5)	6.6±1.1 (5)	36.3±1.7 (5)	22.6±1.5 (5)	62.3±3.9 (5)
15	2.iv.90	40.7±4.8 (3)	15.2±1.7 (3)	6.8±1.7 (3)	37.5±1.8 (3)	23.1±3.8 (3)	61.7±10.4 (3)
	Dispersal						
16	30.iv.90	44.3±3.8 (3)	16.0±0.8 (3)	6.7±0.4 (3)	36.0±1.7 (3)	24.0±0.6 (3)	66.6±1.6 (3)
17	28.v.90	47.6±1.6 (3)	17.6±0.4 (3)	6.9±0.6 (3)	37.2±1.4 (3)	25.6±1.7 (3)	69.2±4.7 (3)

** Significantly different from female value: $P<0.01$

Table 5.2b: Changes in the erythrocyte indices of females born in 1989 (Values are means±1 SD, with number of individuals in parentheses).

TRAPPING SESSION	DATE	HAEMATOCRIT (%)	HAEMAGLOBIN ($g.dl^{-1}$)	10^{12}x RED BLOOD CELLS ($cells.L^{-1}$)	MCHC ($g.dl^{-1}$ red cells)	MCH (pg)	MCV (fl)
	Dispersal						
3	1.v.89	42.1±9.1 (4)	18.0±1.1 (4)	-	44.1±8.6 (4)	-	-
	Winter						
4	29.v.89	43.2±8.4 (4)	13.6±2.8 (4)	6.9±1.1 (4)	31.5±3.5 (4)	20.0±5.0 (4)	63.9±17.4 (4)
5	26.vi.89	46.0±1.7 (5)	18.5±1.0 (5)	6.3±1.9 (5)	40.2±2.4 (5)	31.6±10.7 (5)	78.5±24.9 (5)
6	24.vii.89	50.2±3.0 (5)	19.4±0.5 (5)	7.1±1.7 (5)	38.6±1.9 (5)	28.6±6.4 (5)	74.6±19.8 (5)
7	21.viii.89	44.3±3.5 (5)	17.4±1.1 (5)	7.2±0.4 (5)	39.3±0.8 (5)	24.2±1.9 (5)	61.6±5.6 (5)
8	18.ix.89	46.5±3.9 (6)	17.8±1.6 (6)	7.8±2.0 (6)	38.4±1.3 (6)	23.7±4.8 (6)	61.6±11.1 (6)
9	16.x.89	46.9±4.4 (9)	17.4±1.4 (9)	7.1±0.5 (9)	37.2±2.0 (9)	24.7±1.8 (9)	66.4±4.0 (9)
	Breeding						
10	13.xi.89	48.9±2.9 (8)	18.1±1.1 (8)	7.2±0.8 (8)	37.1±0.8 (8)**	25.3±2.7 (8)	68.4±7.7 (8)
11	11.xii.89	48.7±3.4 (7)	16.9±0.8 (7)	7.2±0.6 (7)	34.9±2.3 (7)	23.6±1.5 (7)	67.8±4.1 (7)
12	8.i.90	42.6±5.5 (5)	15.4±2.0 (5)	7.4±1.4 (5)	36.6±1.1 (5)	20.8±2.3 (5)	57.9±6.8 (5)
13	5.ii.90	37.8±7.2 (5)	14.2±3.1 (5)	5.8±1.7 (5)	37.4±2.4 (5)	24.8±3.2 (5)	66.4±9.7 (5)
14	5.iii.90	40.4±5.2 (4)	15.0±2.1 (4)	7.2±0.9 (4)	37.2±4.4 (4)	20.8±1.3 (4)	56.4±7.7 (4)
15	2.iv.90	37.1 - 44.1 (2)	13.4 - 15.2 (2)	6.0 - 6.6 (2)	34.5 - 36.1 (2)	22.4 - 22.9 (2)	61.9 - 66.3 (2)
	Dispersal						
16	30.iv.90	46.1±2.4 (4)	16.3±0.4 (4)	6.8±0.5 (4)	35.4±2.2 (4)	24.2±1.4 (4)	68.6±5.6 (4)
17	28.v.90	43.6	15.7	7.3	36.1	21.5	59.7

** Significantly different from male value: $P<0.01$

Table 5.3: Changes in the leucocyte indices of individuals born in 1989 (Values are means ± 1 SD, with the number of individuals in parentheses).

		MALES			FEMALES		
TRAPPING SESSION	DATE	10-9 x LEUCOCYTE COUNT (cells.L-1)	NEUTROPHIL (%)	LYMPHOCYTE (%)	10-9 x LEUCOCYTE COUNT (cells.L-1)	NEUTROPHIL (%)	LYMPHOCYTE (%)
	Dispersal						
3	1.v.89	3.1±1.4 (6)			4.5±1.1 (4)	-	-
	Winter						
4	29.v.89	4.9±2.2 (4)	10.2±5.7 (4)	89.8±5.7 (4)	5.6±3.4 (4)	13.0±11.0 (4)	87.0±11.0 (4)
5	26.vi.89	9.7±4.3 (3)	8.3±7.0 (3)	91.7±7.0 (3)	6.7±3.3 (5)	15.0±12.1 (5)	85.0±12.1 (5)
6	24.vii.89	11.1±3.0 (4)	17.8±5.8 (4)	82.2±5.8 (4)	7.6±2.1 (5)	25.2±18.5 (5)	74.8±18.5 (5)
7	21.viii.89	9.9±5.6 (3)	14.0±5.2 (3)	86.0±5.2 (3)	6.8±3.4 (5)	12.2±2.8 (5)	87.8±2.8 (5)
8	18.ix.89	8.1±3.2 (3)	23.3±16.0 (3)	76.7±16.0 (3)	8.1±2.0 (6)	21.8±13.2 (6)	78.2±13.2 (6)
9	16.x.89	11.1±3.9 (5)	16.8±7.3 (5)	83.2±7.3 (5)	8.0±3.5 (7)	12.7±5.8 (7)	87.3±5.8 (7)
	Breeding						
10	13.xi.89	10.8±6.2 (11)	12.7±9.9 (11)	87.3±9.9 (11)	7.1±2.9 (8)	11.4±10.0 (8)	88.6±10.0 (8)
11	11.xii.89	10.2±4.7 (13)	11.2±10.7 (13)	88.8±10.7 (13)	6.4±1.5 (7)	17.3±8.3 (7)	82.3±8.3 (7)
12	8.i.90	11.0±4.9 (8)	6.0±5.6 (8)	94.0±5.6 (8)	4.8±0.6 (5)	-	-
13	5.ii.90	16.8±8.2 (6)	20.5±13.6 (6)	79.5±13.6 (6)	6.2±1.9 (5)	22.8±12.3 (5)	77.2±12.3 (5)
14	5.iii.90	13.0±2.6 (5)	13.2±7.3 (5)	86.8±7.3 (5)	5.6±2.6 (3)	14.8±14.2 (3)	85.2±14.2 (3)
15	2.iv.90	20.9±11.8 (3)	6.3±5.7 (3)	93.7±5.7 (3)	5.8 - 13.1 (2)	-	-
	Dispersal						
16	30.iv.90	18.3±3.0 (3)	4.7±0.6 (3)	95.3±0.6 (3)	16.0±11.2 (4)	16.2±6.2 (4)	83.8±6.2 (4)
17	28.v.90	10.7±2.6 (3)	9.3±2.5 (3)	90.7±2.5 (3)	6.1	5	95

recorded during the 1989 winter (Figure 5.1).

- *MCBC*

MCBC levels did not exceed total corticosterone concentrations during any trapping session and these data should be interpreted with caution. In the winter sessions, concentrations ranging from 3.2±0.4μM (n=5) to 5.6±0.6μM (n=3) were recorded for males. A range of 4.1±1.6μM (n=5) to 6.7±3.5μM (n=3) was recorded for females. Mean concentrations recorded throughout the breeding season for males were lower than for females (males: 1.6μM [n=1] - 2.9±1.4μM [n=5]: females: 4.7±2.9μM [n=4] - 7.9±1.4μM [n=7]).

- *partitioning*

Figure 5.2 and Table 5.4 show partitioning of the corticosterone. Significant differences between absolute levels of biologically active, CBG-bound and albumin-bound corticosterone in males and females were evident during the first three sessions of the breeding season (see Table 5.4 and Appendix 5.4).

Following arcsine $\sqrt{x}$ transformation, the proportions of active and inactive corticosterone in males and females were compared. Inactive (CBG- and albumin-bound) corticosterone concentrations were significantly lower in the males when compared to females at the onset of breeding (see Table 5.5). There was a concomitant increase in the biologically active corticosterone fraction in males at this time and a weakly significant difference ($P<0.05$) was evident between the sexes during December 1989 (Session 11).

5.3.3 The effect of ether on plasma corticosterone concentrations

Concentrations of total, free, CBG-bound and albumin-bound corticosterone are shown in Table 5.6. These levels were not statistically significantly different from values obtained for individuals in the trappable population at the same time.

Haematological parameters were also compared for the two groups (Table 5.7). Significant differences were not recorded for either sex

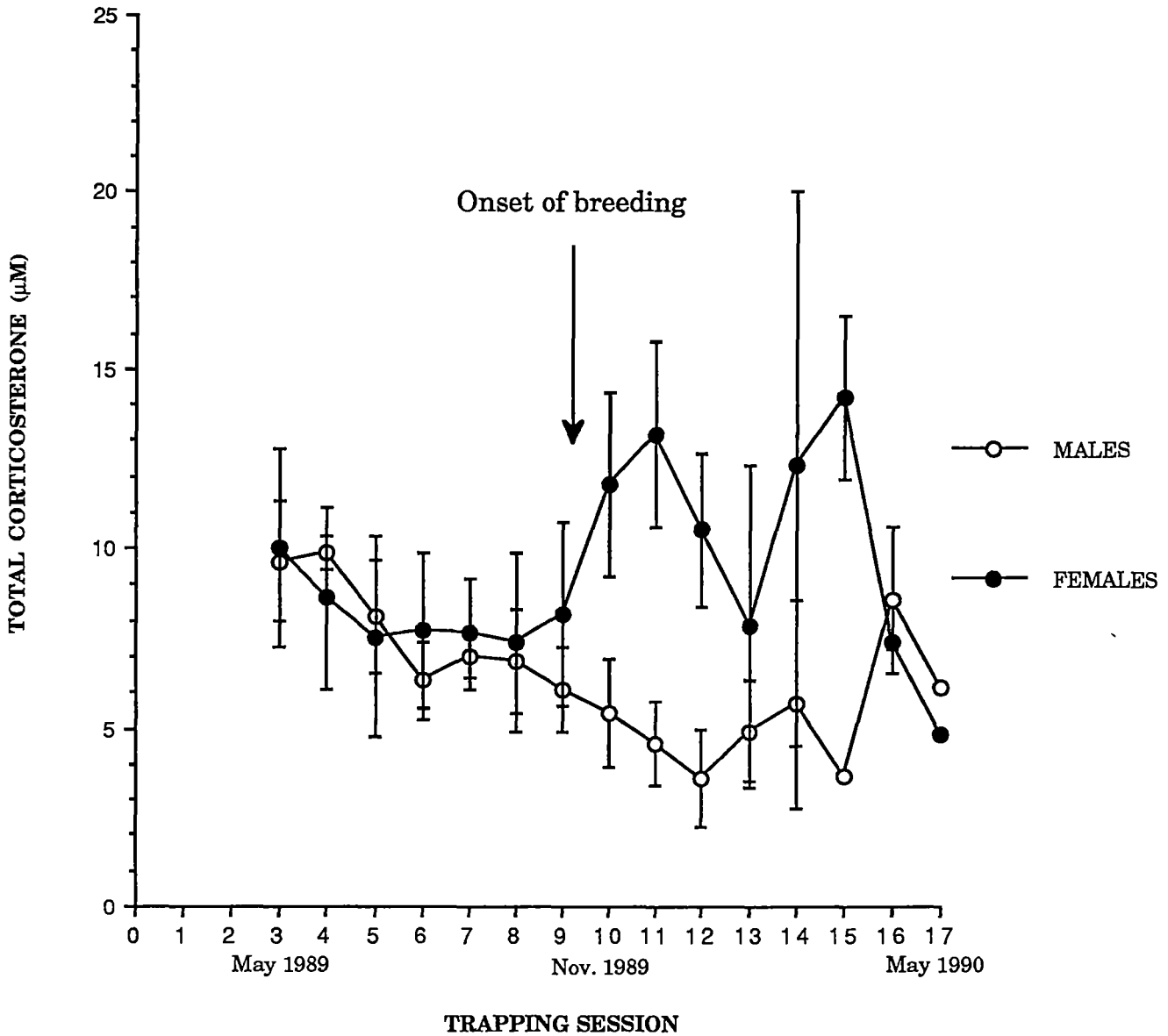


Figure 5.1: The plasma total corticosterone concentration of male and female *R. l. velutinus* born in 1989 (±1 SD, sample sizes are given in Table 5.4).

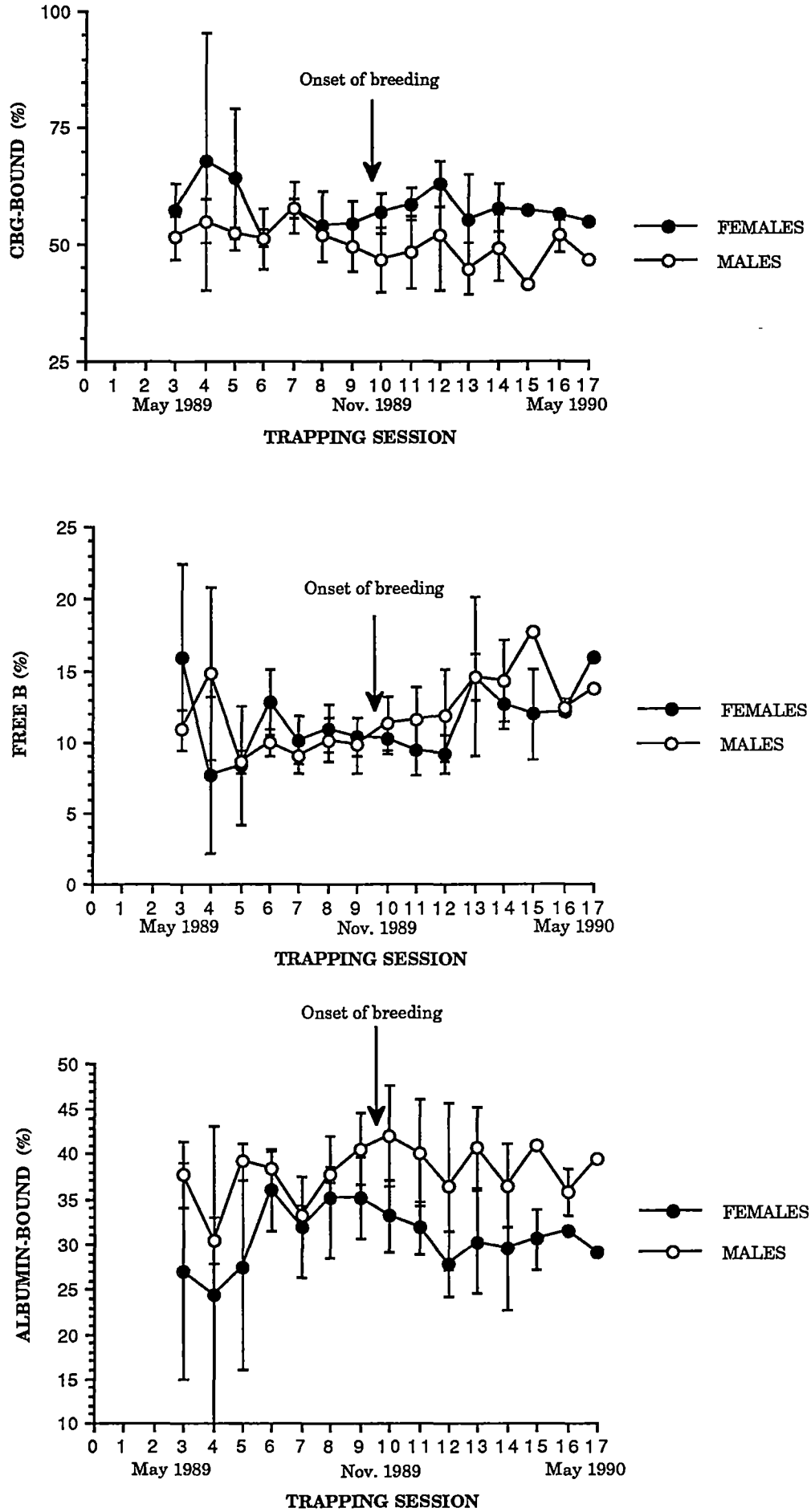


Figure 5.2 a, b & c: The partitioning of plasma corticosterone for each trapping session (± 1 SD, sample sizes are given in Table 5.4).

Table 5.4: Changes in the steroid indices of individuals born in 1989 (Values are means ± 1 SD, with number of individuals in parentheses).

TRAPPING SESSION	DATE	TOTAL CORTICOSTERONE (μM)	MCBC (μM)	FREE CORTICOSTERONE (μM)	CBG BOUND (μM)	ALBUMIN BOUND (μM)
				MALES		
	Dispersal					
3	1.v.89	9.6±1.7 (5)	5.1±0.6 (5)	1.1±0.3 (5)	4.9±0.6 (5)	3.7±0.9 (5)
	Winter					
4	29.v.89	9.9±0.5 (3)	5.6±0.6 (3)	1.5±0 6 (3)	5.4±1.3 (3)	3.0±0.2 (3)
5	26.vi.89	6.6 - 9.7 (2)	3.6 - 5.3 (2)	0.5 - 0.9 (2)	3.5 - 5.1 (2)	2.7 - 3.6 (2)
6	24.vii.89	6.3±1.1 (4)	3.4±0.5 (4)	0.6±0.1 (4)	3.2±0.5 (4)	2.4±0.5 (4)
7	21.viii.89	7.0±0.5 (3)	4.2±0.5 (3)	0.6±0.1 (3)	4.0±0.4 (3)	2.3±0.1 (3)
8	18.ix.89	6.9±1.4 (3)	3.7±0.8 (3)	0.7±0.1 (3)	3.6±0.8 (3)	2.6±0.6 (3)
9	16.x.89	6.1±1.2 (5)	3.2±0.4 (5)	0.6±0.2 (5)	3.0±0.4 (5)	2.5±0.7 (5)
	Breeding					
10	13.xi.89	5.4±1.5 (11)	2.6±0.7 (11)	0.6±0.2 (11)	2.5±0.7 (11)	2.3±0.8 (11)
11	11.xii.89	4.6±1.2 (13)	2.3±0.6 (13)	0.5±0.1 (13)	2.2±0.6 (13)	1.9±0.6 (13)
12	8.i.90	3.6±1.4 (8)	1.9±0.4 (8)	0.4±0.2 (8)	1.7±0.4 (8)	1.4±0.8 (8
13	5.ii.90	4.9±1.4 (6)	2.3±0.4 (6)	0.7±0.3 (6)	2.2±0.4 (6)	2.0±0.8 (6)
14	5.iii.90	5.7±2.9 (5)	2.9±1.4 (5)	0.8±0.6 (5)	2.8±1.4 (5)	2.0±1.0 (5)
15	2.iv.90	3.7 (1)	1.6 (1)	0.7 (1)	1.5 (1)	1.5 (1)
	Dispersal					
16	30.iv.90	8.6±2.1 (3)	4.6±1.3 (3)	1.1±0.2 (3)	4.5±1.3 (3)	3.0±0.6 (3)
17	28.v.90	6.1 - 6.2 (2)	2 5 - 3 5 (2)	0.8 - 1.0 (2)	2.4 - 3.4 (2)	2.1 - 2.8 (2)
				FEMALES		
	Dispersal					
3	1.v.89	10.0±2.7 (3)	5.9±2.2 (3)	1.7±1.1 (3)	5.8±2.2 (3)	2.5±0.6 (3)
	Winter					
4	29.v.89	8.6±2.5 (3)	6.7±3.5 (3)	0.7±0.6 (3)	5.9±0.5 (3)	2.0±1.6 (3)
5	26.vi.89	7.5±2.8 (4)	5.1±1.4 (4)	0 7±0 5 (4)	4.6±1.3 (4)	2.2±1.3 (4)
6	24.vii.89	7.7±2.2 (5)	4.1±1.6 (5)	1.0±0.3 (5)	4.0±1.5 (5)	2.7±0.7 (5)
7	21.viii.89	7.6±1.5 (5)	4.6±1.2 (5)	0 8±0.2 (5)	4.4±1.2 (5)	2 4±0 4 (5)
8	18.ix 89	7.4±2 5 (5)	4.2±1.7 (5)	0.8±0.3 (5)	4 1±1.7 (5)	2.5±0.6 (5)
9	16.x.89	8.2±2.5 (7)	4.6±1.6 (7)	0.9±0 3 (7)	4.5±1.6 (7)	2 8±0.8 (7)
	Breeding					
10	13.xi.89	11 8±2 6 (8)	6.9±1.7 (8)	1.2±0.2 (8)	6.7±1.7 (8)	3.9±0.8 (8)
11	11.xii.89	13 2±2.6 (7)	7.9±1.4 (7)	1 3±0 5 (7)	7.7±1.4 (7)	4.2±0.8 (7)
12	8 i.90	10.5±2.1 (5)	6.9±1.7 (5)	0.9±0.1 (5)	6.7±1.6 (5)	2.9±0.5 (5)
13	5.ii.90	7.8±4.5 (4)	4.7±2.9 (4)	1 0±0 6 (4)	4.5±2.8 (4)	2.3±1.2 (4)
14	5.iii.90	12.3±7.8 (3)	7 3±4.4 (3)	1.6±1 0 (3)	7.1±4.4 (3)	3.5±2.5 (3)
15	2.iv.90	11.9 - 16.5 (2)	7 0 - 9 6 (2)	1.6 - 1.7 (2)	6.9 - 9.4 (2)	3.4 - 5.4 (2)
	Dispersal					
16	30.iv.90	7.3 - 7.5 (2)	4 3 - 4 4 (2)	0 7 - 1.1 (2)	4.1 - 4.2 (2)	2.2 - 2.5 (2)
17	28.v.90	4 9 (1)	2.8 (1)	0.8 (1)	2 7 (1)	1.4 (1)

Table 5.5: The partitioning of plasma corticosterone for individuals born in 1989 (Values are means±1 SD, with the number of individuals in parentheses).

TRAPPING SESSION	DATE		PARTITIONED CORTICOSTERONE			ARCSINE√x TRANSFORMATION		
			FREE (%)	CBG BOUND (%)	ALBUMIN BOUND (%)	FREE (radians)	CBG BOUND (radians)	ALBUMIN BOUND (radians)
	Dispersal							
3	1.v.89	Female (3)	15.9±6.5	57.1±5.8	27.0±12.0	0.40±0.08	0.86±0.06	0.54±0.15
		Male (5)	10.9±1.4	51.4±4.7	37.7± 3.7	0.34±0.02	0.80±0.05	0.66±0.04
					d.f.=6	**t=1.829 P=0.1171**	**t=1.514 P=0.1808**	**t=1.863 P=0.1118**
	Winter							
4	29.v.89	F (n=3):	7.7±5.6	67.9±27.8	24.4±18.7	0.26±0.12	1.00±0.30	0.48±0.26
		M (n=3)	14.8±6.0	54.9±4.6	30.4±2.6	0.39±0.09	0.83±0.05	0.58±0.03
					d.f.=4	**t=1.404 P=0.2330**	**t=0.948 P=0.3969**	**t=0.669 P=0.5403**
5	26.vi.89	F (n=4)	8.4±4.2	64.1±15.3	27.5±11.5	0.28±0.09	0.94±0.18	0.54±0.14
		M (n=2)	8.1 - 9.3	51.3 - 53 0	37.7 - 40.6	0.30±0.01	0.81±0.01	0.68±0.02
					d.f.=4	**n.a.***	**n.a.**	**n.a.**
6	24.vii.89	F (n=5)	12.9±2.3	51.2±6.6	36.0±4.6	0.37±0.03	0.80±0.07	0.64±0.05
		M (n=4)	10.0±1.0	51.2±1 8	38.4±1.9	0.32±0.02	0.80±0.02	0.67±0.02
					d.f.=7	**t=2.314 P=0.0539**	**t=0.103 P=0.9208**	**t=0.964 P=0.3674**
7	21.viii.89	F (n=5)	10.2±1.7	57.8±5.4	32.0±5.6	0.32±0.03	0.86±0.06	0.60±0.06
		M (n=3)	9.1±1.3	57.7±2.1	33.2±1.2	0.31±0.02	0 86±0.02	0.61±0.01
					d.f.=6	**t=0.911 P=0.3973**	**t=0.024 P=0.9819**	**t=0.359 P=0.7317**
8	18.ix.89	F (n=5)	11.0±1.7	53.8±7.5	35.2±6.8	0.34±0.03	0.82±0.08	0.63±0.07
		M (n=3)	10.2±1.5	52.0±1.0	37.8±0.9	0.32±0.02	0.81±0.01	0.66±0.01
					d.f.=6	**t=0.734 P=0.4905**	**t=0.394 P=0.7075**	**t=0.663 P=0.5322**
9	16.x.89	F (n=7)	10.4±1.4	54 3±4 8	35.2±4.5	0.33±0.02	0.83±0.05	0.64±0.05
		M (n=5)	9.8±1.9	49.6±5.4	40.6±4.0	0.32±0.03	0.78±0.05	0.69±0.04
					d.f.=10	**t=0.740 P=0.4762**	**t=1.589 P=0.1432**	**t=2.113 P=0.0608**

Table 5.5 cont.: The partitioning of plasma corticosterone for individuals born in 1989 (Values are means±1 SD, with the number of individuals in parentheses).

TRAPPING SESSION	DATE		PARTITIONED CORTICOSTERONE			ARCSINE√x TRANSFORMATION		
			FREE (%)	CBG BOUND (%)	ALBUMIN BOUND (%)	FREE (radians)	CBG BOUND (radians)	ALBUMIN BOUND (radians)
	Breeding							
10	13.xi.89	F (n=8)	10.3±1.1	56.6±4.2	33.2±4.0	0.33±0.02	0.85±0.04**	0.61±0.04**
		M (n=11)	11.3±1 9	46.6±6.8	42.1±5.6	0.34±0.03	0.75±0.07**	0.70±0.06**
					d.f.=17	t=1.34 P=0.1980	t=3.607 P=0.0022	t=3.825 P=0.0014
11	11.xii.89	F (n=7)	9.5±1.8	58.6±3.5	31.9±2.9	0.31±0.03*	0.87±0.04**	0.60±0.03**
		M (n=13)	11.6±2.3	48.2±7.6	40.2±5.9	0.35±0.04*	0.77±0.08**	0.69±0.06**
					d.f=18	t=2.11 P=0.0491	t=3.371 P=0.0034	t=3.510 P=0.0025
12	8.i 90	F (n=5)	9 2±1.4	63.0±4.8	27.8±3.7	0.31±0.02	0.92±0.05	0.55±0.04
		M (n=8)	11.9±3.3	51.7±11.6	36.4±9 2	0.35±0 05	0.80±0.12	0.64±0.10
					d.f.=11	t=1.643 P=0.1286	t=1.993 P=0.0716	t=1.904 P=0.0833
13	5.ii.90	F (n=4)	14.6±5.6	55.1±10.0	30.3±5.7	0.39±0.08	0 84±0.10	0.58±0.06
		M (n=6)	14.6±1.6	44.7±5.5	40 8±4.5	0.39±0.02	0.73±0.06	0.69±0.05
					d.f.=8	t=0.123 P=0.9048	t=2.162 P=0.0626	t=3.251 P=0.0117
14	5.iii 90	F (n=3)	12.7±1.8	57.7±5.1	29.5±6 8	0.36±0.03	0.86±0.05	0.57±0.08
		M (n=5)	14.3±2.8	49.2±7.0	36.5±4.6	0.39±0.04	0.78±0.07	0 65±0.05
					d.f.=6	t=0.859 P=0.4234	t=1.835 P=0.1161	t=1.739 P=0.1327
15	2.iv.90	F (n=2)	9.7 - 14.2	57.3 - 57.5	28.3 - 33.0	0.32 - 0.39	0.86	0.56 - 0.61
		M (n=1)	17.7	41.4	40.9	0.44	0.70	0.69
					d.f.=1	n.a.	n.a.	n.a.
	Dispersal							
16	30.iv.90	F (n=2)	9.6 - 14.7	56 2 - 56.7	29.2 - 33 7	0.32 - 0.39	0 85	0.57 - 0.62
		M (n=3)	12.5±0.6	51.7±3 3	35.8±2.6	0.36±0.01	0 80±0.03	0.64±0.03
					d.f.=3	n.a.	n.a.	n.a.
17	28.v 90	F (n=1)	16 0	54.8	29 2	0.41	0.83	0.57
		M (n=2)	12.0 - 15.6	38.8 - 54.7	33.3 - 45.6	0.35 - 0.41	0 67 - 0.83	0.62 - 0.74
					d.f.=1	n.a.	n.a.	n.a.

* n.a.: not analysed - sample size too small. ** P<0.01 see text for discussion.

Table 5.6: Concentrations of plasma corticosterone for individuals in trapping session six and the ether-effect experiment. No significant differences were detected between sexes or sessions. Values are means ± 1 SD, with number of individuals in parentheses.

SESSION	TOTAL B (μM)	MCBC (μM)	FREE (μM)	CBG BOUND (μM)	ALBUMIN BOUND (μM)
			MALES		
VALIDATION (18.vii.89 - 13.viii.89)	4.8±1.6 (5)	2.3±0.9 (5)	0.6±0.2 (5)	2.2±0.9 (5)	2.0±0.6 (5)
			FEMALES		
	5.7±1.5 (9)	3.5±2.0 (9)	0.6±0.2 (9)	3.2±1.6 (9)	1.9±0.8 (9)
d.f.=12	t=0.058 P=0.311	t=1.228 P=0.243	t=0.099 P=0.923	t=1.309 P=0.215	t=0.242 P=0.813
			MALES		
VALIDATION (18.vii.89 - 13.viii.89)	4.8±1.6 (5)	2.3±0.9 (5)	0.6±0.2 (5)	2.2±0.9 (5)	2.0±0.6 (5)
SIX (24.vii.89 - 28.vii.89)	6.3±1.1 (4)	3.4±0.5 (4)	0.6±0.1 (4)	3.2±0.5 (4)	2.4±0.5 (4)
d.f.=8	t=1.628 P=0.148	t=2.354 P=0.051	t=0.311 P=0.765	t=2.255 P=0.059	t=1.124 P=0.298
			FEMALES		
VALIDATION (18.vii.89 - 13.viii.89)	5.7±1.5 (9)	3.5±2.0 (9)	0.6±0.2 (9)	3.2±1.6 (9)	1.9±0.8 (9)
SIX (24.vii.89 - 28.vii.89)	7.7±2.2 (5)	4.1±1.6 (5)	0.9±0.3 (5)	4.0±1.5 (5)	2.7±0.7 (5)
d.f.=12	t=2.019 P=0.067	t=0.622 P=0.546	t=2.019 P=0.067	t=0.945 P=0.363	t=1.971 P=0.072

Table 5.7: Haematological parameters from individuals from trapping session six and the ether validation experiment (Values are means ± 1SD). There were no significant differences within parameters by sex or by group (see Appendix 5.7).

BLOOD PARAMETER	VALIDATION		SESSION SIX	
	FEMALES (n=9)	MALES (n=6)	FEMALES (n=5)	MALES (n=4)
HAEMATOCRIT (%)	43.9±4.4	47.0±1.8	50.2±3.0	48.6±2.8
PROTEIN ($g.dl^{-1}$)	6.9±0.6	6.8±1.0	7.0±0.5	7.4±0.6
HAEMOGLOBIN ($g.dl^{-1}$)	17.8±2.4	18.5±1.0	19.3±0.5	18.6±0.7
10^{-12} x RED CELL COUNT ($cells.L^{-1}$)	6.5±0.8	7.2±1.1	7.1±1.7	6.2±0.5
MCHC ($g.dl^{-1}$ red cells)	41.1±7.6	39.2±2.9	38.6±1.9	38.3±1.0
MCH (pg)	28.0±5.1	26.2±4.4	28.5±6.4	30.5±3.7
MCV (fL)	69.3±14.7	66.8±10.2	74.6±19.8	79.7±11.4
10-9 x LEUCOCYTE COUNT ($cells.L^{-1}$)	8.4±2.9	12.7±7.7	7.6±2.1	11.1±3.0
LYMPHOCYTES (%)	74.3±20.3	90.5±7.6	74.8±18.5	80.2±7.9
NEUTROPHILS (%)	25.7±20.3	9.9±7.6	25.2±18.5	19.8±7.9

(Appendix 5.5).

5.3.4 Tail-scarring and ectoparasite burdens

Table 5.8 presents data on the incidence of tail-scarring and obvious burdens of ectoparasites recorded during each trapping session. Tail scarring was the most prevalent form of wounding seen in *R. l. velutinus,* although occasionally blood from flank wounds was noted.

Scarring was observed infrequently during the winter. One sub-adult female was captured with a recent tail wound in June 1989 and another female had a recent scar when trapped in October 1989. There was no evidence of tail-scarring in males throughout the winter.

In January 1990, a marked increase in tail-scarring was observed for males. Seven of nine individuals captured had recent tail wounds; two animals had the tips of their tails missing. No tail-scarred female was captured at this time. Four weeks later all males (n=9) trapped had either the tips of their tails missing or increased numbers of tail wounds. Two of six females were also trapped with tail wounds. The next trapping session resulted in fewer adult males being captured (n=5) but all had recent tail damage.

Ectoparasite burdens were not quantified in any way during the study. However, obvious burdens of a predacious beetle larvae (*Myotyphlus jansoni*) were common on some males captured in poor condition. These larvae have been reported from *R. l. velutinus* previously (Britton 1978). Large infestations occurred on three individuals early in the study and in all cases the individual was not captured again. In each case, larvae were observed in high numbers on the lower back immediately above the tail.

During March and April 1990, very large burdens of ectoparasites were observed on adult males. Ixodid ticks were apparent in large numbers on the faces and around the ears of affected individuals and *M. jansoni* larvae were again common close to the tail. In all cases, these parasite loads coincided with fur thinning or loss. No male observed in this condition was trapped again.

Table 5.8: The incidence of tail scarring and large ectoparasite burdens recorded during each trapping session.

TRAPPING SESSION	DATE	LIFE HISTORY EVENTS	TAIL SCARS		ECTOPARASITE BURDENS
			MALES	FEMALES	
	Dispersal				
1	20.iii.89		1 (2 scars)	1 (1 scar)	1 male x excess *M. jansoni*
2	4.iv.89		1 (2 scars)	1 (1 scar)	
3	1.v.89		1 (2 scars)	-	
	Winter				
4	29.v.89		-	1 (1 scar)	1 male x excess *M. jansoni*
5	26.vi.89		-	-	
6	24.vii.89		-	-	1 male x excess *M. jansoni*
7	21.viii.89		-	-	
8	18.ix.89		-	-	
9	16.x.89		-	-	
	Breeding				
10	13.xi.89	All males captured with scrotal testes	-	-	
11	11.xii.89	First lactating females recorded	2 (1 scar each)	-	
12	8.i.90		7 (4 single/ 3 multiple) 1 (end missing)	-	
13	5.ii.90	First young of 1990 enter trappable population	9 (1 single/ 8 multiple) 2 (end missing)	2 (end missing)	
14	5.iii.90		5 (5 multiple/ 1 end missing)	-	All x excess *M. jansoni* & ixodid ticks
15	2.iv.90		3 (3 multiple/ 3 ends missing)	-	2 male x excess *M. jansoni* & ixodid ticks
	Dispersal				
16	30.iv.90		1 (end missing)	-	1 male x excess ixodid ticks
17	28.v.90		1 (end missing)	1 (1 scar)	

5.3.5 The effects of habitat on 'condition'

The condition indices described above present a profile for similar-aged individuals of each sex from a time shortly after weaning when individuals first enter the trappable population until a period following the breeding season when these individuals were no longer captured. These data are of interest in their own right but in the context of this thesis it is necessary to examine the morpho-physiological parameters of all individuals in the trappable population. If few differences exist between mean values regardless of sex or age, then direct comparisons can be made between individuals captured in particular habitat groups. The effects of heterogeneous habitat on the ecophysiology of *R. l. velutinus* can then be quantified.

It was during the winter that differential habitat use was most apparent (see Chapter 4) and so analyses are restricted to data collected during these six trapping sessions.

Few differences in conditional indices were apparent between sexes for the 1989 cohort during winter. At this time, individuals are sub-adult and it appears that males and females share similar haematological and corticosteroid profiles.

Few data were collected from adults which survived beyond the 1988/ 1989 breeding season (Appendix 7). However, where sample sizes were sufficient these data were compared with values obtained during the winter (see Appendix 8). These comparisons revealed a significant difference in haematocrit (adults< sub-adults: $t=3.712$, d.f.=7, $P=0.0075$) and haemoglobin concentration (adults< sub-adults: $t=4.499$, d.f.=7, $P=0.0028$) between adult and sub-adult females during July 1989 (session six). This was caused by higher than normal values recorded for the sub-adults and it is likely that these values are aberrant. All other comparisons revealed little difference between mean values for all other blood parameters. Consequently, condition data for males and females, adults and sub-adults were grouped and the physiological states of individuals active (i.e., captured) in habitat group 1a were compared with individuals captured in the other habitat groups using unpaired t-tests. The results of these comparisons are

Table 5.9: Haematological parameters for all individuals active in different habitat groups (Values are means+1 SD, with the number of individuals in parentheses).

TRAPPING SESSION	DATE	HABITAT GROUP	HAEMATOCRIT (%)	HAEMOGLOBIN CONCENTRATION (g/dL)	TOTAL PROTEIN (g/dL)	10^{12}x RED BLOOD COUNT (cells.L^{-1})	10^{9}x WHITE BLOOD COUNT (cells.L^{-1})
	Winter						
4	29.v.89	1a	39.7±7.2 (3)	15.8±3.9 (3)	7.3±0.3 (3)	-	6.5±4.7 (3)
		1b, 2 & 3	48.5±4.6 (9)	15.3±1.9 (9)	7.0±0.7 (9)	-	6.3±3.3 (9)
		d.f.=10	**t=2.500 P=0.032**	**t=0.241 P=0.814**	**t=0.532 P=0.606**	-	**t=0.105 P=0.918**
5	26.vi.89	1a	46.4±1.8 (5)	18.0±1.2 (5)	7.3±0.8 (5)	6.8±1.9 (5)	4.9±2.1 (5)
		1b, 2 & 3	45.3±3.3 (8)	18.5±1.4 (8)	7.1±0.8 (8)	6.8±1.6 (8)	9.5±4.9 (8)
		d.f.=11	**t=0.621 P=0.547**	**t=0.596 P=0.564**	**t=0.461 P=0.654**	**t=0.050 P=0.961**	**t=1.951 P=0.077**
6	24.vii.89	1a	43.7±6.0 (6)	17.4±1.8 (6)	7.7±0.6 (6)	7.0±0.7 (6)	8.2±2.6 (6)
		1b, 2 & 3	48.8±3.4 (8)	18.8±1.0 (8)	7.2±0.7 (6)	7.0±1.6 (8)	8.2±3.8 (8)
		d.f.=12	**t=2.051 P=0.063**	**t=1.955 P=0.074**	**t=1.429 P=0.179**	**t=0.018 P=0.986**	**t=0.022 P=0.983**
7	21.viii.89	1a	44.0±1.4 (5)	17.7±0.5 (5)	7.6±0.5 (5)	7.8±0.9 (5)	7.7±3.1 (5)
		1b, 2 & 3	44.3±1.8 (8)	17.7±1.5 (8)	7.1±0.7 (8)	7.8±1.4 (8)	7.9±4.1 (8)
		d.f.=11	**t=0.136 P=0.894**	**t=0.010 P=0.992**	**t=1.478 P=0.167**	**t=0.045 P=0.9648**	**t=0.080 P=0.9376**
8	18.ix.89	1a	42.3±1.4 (3)	16.7±1.2 (3)	7.1±0.5 (3)	6.9±0.8 (3)	6.8±2.2 (3)
		1b, 2 & 3	46.0±3.7 (10)	17.6±1.5 (10)	7.3±0.4 (10)	8.0±1.7 (10)	8.7±3.9 (10)
		d.f.=11	**t=1.639 P=0.129**	**t=0.966 P=0.355**	**t=0.728 P=0.482**	**t=1.093 P=0.298**	**t=0.785 P=0.449**
9	16.x.89	1a	47.4±3.8 (4)	17.8±0.7 (4)	7.6±0.7 (4)	7.2±0.4 (4)	5.3±0.4 (4)
		1b, 2 & 3	48.2±5.3 (11)	17.4±1.9 (11)	6.9±0.7 (11)	7.1±0.6 (11)	9.8±3.7 (11)
		d.f.=13	**t=0.260 P=0.799**	**t=0.406 P=0.692**	**t=1.751 P=0.104**	**t=0.505 P=0.622**	**t=2.356 P=0.035**

Table 5.10: Corticosterone fractions for individuals active in different habitat groups (Values are means±1 SD, with the number of individuals in parentheses).

TRAPPING SESSION	DATE	HABITAT GROUP	PARTITIONED CORTICOSTERONE FREE (radians)	CBG-BOUND (radians)	ALBUMIN-BOUND (radians)
	Winter				
4	29.v.89	1a	0.36±0.0 (3)	0.83±0.03 (3)	0.62±0.04 (3)
		1b, 2 & 3	0.33±0.11 (7)	0.93±0.20 (7)	0.52±0.16 (7)
		d.f.=8	**t=0.399 P=0.702**	**t=0.675 P=0.521**	**t=0.793 P=0.454**
5	26.vi.89	1a	0.26±0.10 (5)	1.00±0.25 (5)	0.49±0.21 (5)
		1b, 2 & 3	0.31±0.02 (6)	0.86±0.05 (6)	0.61±0.06 (6)
		d.f.=9	**t=1.243 P=0.245**	**t=1.331 P=0.216**	**t=1.330 P=0.216**
6	24.vii.89	1a	0.34±0.03 (6)	0.82±0.06 (6)	0.63±0.04 (6)
		1b, 2 & 3	0.34±0.04 (8)	0.81±0.06 (8)	0.64±0.05 (8)
		d.f.=12	**t=0.346 P=0.736**	**t=0.456 P=0.657**	**t=0.425 P=0.678**
7	21.viii.89	1a	0.32±0.03 (6)	0.86±0.05 (6)	0.61±0.06 (6)
		1b, 2 & 3	0.31±0.02 (7)	0.87±0.05 (7)	0.60±0.05 (7)
		d.f.=11	**t=0.692 P=0.503**	**t=0.495 P=0.630**	**t=0.285 P=0.781**
8	18.ix.89	1a	0.33±0.03 (4)	0.85±0.01 (4)	0.61±0.03 (4)
		1b, 2 & 3	0.32±0.03 (8)	0.82±0.07 (8)	0.64±0.06 (8)
		d.f.=10	**t=0.554 P=0.592**	**t=0.760 P=0.464**	**t=1.028 P=0.328**
9	16.x.89	1a	0.32±0.03 (4)	0.82±0.02 (4)	0.64±0.03 (4)
		1b, 2 & 3	0.32±0.03 (11)	0.82±0.08 (11)	0.64±0.07 (11)
		d.f.=13	**t=0.276 P=0.787**	**t=0.012 P=0.991**	**t=0.125 P=0.902**

presented in Tables 5.9 and 5.10.

5.4 Discussion

The measurement of certain blood parameters throughout the post-weaning lives of individuals born in 1989 allowed the detection of changes related to age, sex and seasonal differences. With no 'normal' values for comparison, however, it is not possible to draw conclusions about whether these values are representative of *R. l. velutinus* in general.

Despite this, it is still worthwhile to examine the physiological profiles of the individuals in the trappable population. Table 5.11 presents a schematic representation of the major physiological 'events' recorded for individuals of the 1989 cohort throughout the study.

Intraspecific variation has been recorded for most mammalian blood parameters and has been related to various extrinsic as well as intrinsic factors which may alter an individual's physiology (e.g., Sealander 1964, 1966; Lee and Brown 1970; Maclean and Lee 1973; Barnett *et al.* 1979a, 1979b).

Changes with age occurred in mean plasma albumin concentration, haemoglobin concentration, mean red cell and white cell counts in females, and mean white cell count in males. All other parameters fluctuated over time for each sex (see Tables 5.1, 5.2 and 5.3).

Female mean albumin and haemoglobin concentrations and erythrocyte and leucocyte counts declined during the breeding season. These changes were most likely due to pregnancy and lactation. At this time, immune functions are depressed, albumin levels are lowered during lactation and dietary and microcytic anaemias are common. The recorded decline in MCV (see Table 5.2) reinforces the likelihood of a microcytic anaemia in females in the trappable population (A. Macfadyen, pers. comm.).

Mean male leucocyte count rose markedly at the end of the breeding season. Obvious burdens of ectoparasites were observed on most males and individuals which had been captured repeatedly throughout the study were no longer entering traps. The final three trapping sessions resulted in the trapping of only three adult males and it is likely that the post-breeding

SEASON	DISPERSAL	WINTER	BREEDING	POST-BREEDING
MALES	Weaned young first enter the trappable population.		Marked increase in mean body weight. Decline in haemoglobin and MCHC concentration Decline in mean total corticosterone concentration but an increase in the biologically-active fraction.	Continued increase in mean leucocyte count. Obvious ectoparasite burdens Fur-thinning and loss. Residents no longer in trappable population.
		No intersexual differences in haematological and corticosterone profiles. Steady rise in body weight.		
FEMALES	Weaned young first enter the trappable population.		Decline in mean leucocyte count. Significant increase in mean total corticosterone concentration but an actual decline in the biologically-active fraction.	

Table 5.11: Schematic representation of the major physiological 'events' recorded for individual *R. l. velutinus* from the 1989 cohort.

period is one of high mortality amongst adult males (discussed later).

Significant differences between the mean values of male and female blood parameters were uncommon. Mean plasma albumin concentration was significantly higher in males during one winter trapping session (July 1989: t=3.896, d.f.=7, P=0.0059). This was unexpected and difficult to explain. Decreased albumin concentration in females may reflect a nutritional stress but this is not supported by the levels of total plasma proteins recorded at the same time. It is more likely an aberration due to low sample sizes.

Mean male MCHC levels declined at the onset of breeding and differed significantly from mean female concentrations (t=3.062, d.f.=17, P=0.0071). Such a decline may be attributable to an increase in growth in males. Body weights rose markedly at this time (see Section 2.4.1) and a concomitant drop in haemoglobin concentration would be anticipated. All other haematological parameters showed little variation between sexes.

The endocrinological values obtained from ether-stressed individuals did not differ significantly from values for individuals in the trappable population at the same time. This indicates that the routine handling and bleeding protocol used in this study acted to mask 'resting' levels of circulating corticosterone. The mean levels of total plasma corticosterone obtained for *R. l. velutinus* were marginally higher than those reported by Barnett (1977) and McDonald *et al.* (1988) for *R. fuscipes* which had also been subjected to ether stress and it is likely that the values for both *Rattus* spp. represent maximal adrenal corticosterone release. It is not necessary (or possible) to demonstrate unstimulated adrenocortical activity, nor is it relevant when examining the seasonal effects of a stressful environment. The monitoring of maximal adrenal corticosterone release offers insights into the susceptibility of individuals to the effects of stress throughout the year (Lee and McDonald 1985).

Excessive adrenocortical response to stressors has been correlated with immunosuppression and disease in some small mammals and coincides with a time when the mean concentration of total plasma corticosterone exceeds MCBC (e.g., *Antechinus* spp.; Bradley *et al.* 1980; McDonald *et al.* 1981, 1986; and *Phascogale calura*; Bradley 1987). This indicates an inability to bind and render inactive circulating corticosterone. A

consequent increase in free corticosterone acts to suppress immune and inflammatory responses leading to disease and death.

In this study, MCBC levels were inexplicably low. Great care was taken during the assaying procedures but it was not possible to determine where an error was made. Consequently, it was not possible to predict accurately at what time of the year each sex was most affected by stress. Despite this, comparisons between the partitioned fractions and total plasma corticosterone were still useful in interpreting whether individuals were less able to cope with the imposition of an acute stressor at any particular time.

The decline in mean total corticosterone concentrations recorded for males at the onset of breeding reflects an androgen-dependent suppression of adrenocorticosteroid production (A.J. Bradley, pers. comm.). However, throughout the breeding season the free corticosterone fraction was consistently higher than for females indicating that, even with a decline in total corticosterone production, males were less able to cope with stresses associated with reproduction.

The increase in mean female corticosterone concentrations ~~concentrations~~ during the breeding season reflects a general increase in corticosteroid production during pregnancy (Schulster *et al.* 1976). The elevated levels are due mainly to the oestrogen-mediated synthesis of increased concentrations of CBG which results in a greater proportion of CBG-bound corticosterone (Johnson and Everitt 1988: see Figure 5.2b). The double peaks of total plasma corticosterone shown in Figure 5.1 for females may reflect the two litters that most individuals have in the breeding season.

The fraction of albumin-bound corticosterone also increased during the breeding season so that the percentage of biologically active corticosterone actually declined (Table 5.5).

The levels and timing of wounding throughout the year are of interest. The marked increase in scarring arising, presumably, from increased aggressive encounters occurred in the middle of the breeding season. Only males were captured with recent tail scars in December 1989 and January 1990 when lactating females were first captured. In February 1990, every male captured (n=9) showed evidence of recent wounds. This time coincided with the period prior to and during the weaning of first litters and it is

thought that such wounding results from aggressive female-male encounters rather than male-male fighting (R. K. Rose, pers. comm.). If this is the case, it is most likely a mechanism whereby females are able to defend resources necessary for ensuring the survival of their offspring, and possibly to prevent infanticide (Ostfeld 1990).

Towards the end of the breeding season, the increased free corticosterone concentration recorded in males coincided with an increase in total leucocyte counts, a reduction in lymphocyte number (lymphocytopenia), a proportional increase in neutrophils (neutrophilia), weight loss and an increased prevalence of ectoparasites. All these conditional indices reflect a time of increased disease and mortality following breeding.

Parasites, by definition, debilitate their hosts and may lead to decreased host survival rates. Ectoparasites depress fitness in four principal ways: disease transmission; removal of lymph and blood from the host; tissue damage; and by increasing the time a host needs to spend grooming (Hoogland 1979). Although few quantifiable data were recorded, it is probable that the marked increase in the number of ectoparasites seen at this time may play some role in the senescence inferred in the males.

Unfortunately, at this time of the year sample sizes were very low (<5 adult males trapped between March and June 1990) and individual variation for many parameters was great. What was apparent was that individuals which appeared in poor condition outwardly, displayed signs of abnormal physiology and dropped out of the trappable population.

Comparison of physiological parameters from individuals active in different habitat groups during the 1989 winter did not reveal any significant differences. This suggests that individuals captured in 'peripheral' habitat are able to cope as well as individuals located in 'preferred' habitat. One possible explanation for this result may lie in the analysis itself. No information was collected about core activity areas within home ranges. It was not possible to determine where individuals lived or what they were doing in a particular area immediately prior to capture. No conclusions can be drawn about possible effects of habitat on the ecophysiology of *R. l. velutinus* if it is not known whether each individual was captured in an area where it was resident.

What is apparent from these analyses, however, is the stability of the parameters measured. Many individuals had very similar physiological profiles, irrespective of their age, sex or where they were captured. It is likely that the areas of preferred habitat have the most resources and will carry more individuals. Others survive equally well in peripheral areas, but at lower densities.

CHAPTER SIX
GENERAL DISCUSSION

6.1 Introduction

This study investigated differential habitat use by a local population of *R. l. velutinus* using capture-mark-recapture and some ecophysiological techniques. The study was conducted to test an initial hypothesis that fewer males entered a trappable population during winter. Live-trapping began in March 1989 at a time when adults were in breeding condition and weaned young were first entering the trappable population. The study continued for 15 months until June 1990 when the young of 1989 had matured, bred and were then no longer part of the trappable population. Throughout the trapping program, the majority of individuals were trapped repeatedly. Regular sampling enabled valuable insights into social spacing and habitat use, and the trapping methods employed (i.e., grid size, grid location) were tested for possible biases in trappability.

Four heterogeneous habitat groups within a wet sclerophyll formation were defined using floristic and structural parameters and the frequency of capture of individuals within each habitat group was compared. A preference for areas of densest cover to one metre height (vegetation, rocks and logs) was recorded for each sex when captures were correlated with habitat features. A strong association of female captures in the habitat groups with densest cover was found throughout the study and is of special interest.

In this Chapter, the results presented in this thesis are combined and an integrated assessment of the habitat preferences and ecophysiology of a successful, but rarely studied, small Tasmanian mammal is made.

6.2 Trappability

Live-trapping permits insights into habitat use by free-living communities of small mammals. However, as a technique it has inherent deficiencies. An individual will only be captured if it 'chooses' to enter a trap (Stoddart 1982). Thus, live-trapping must not be viewed as random

sampling; individuals effectively 'sample themselves' (Wallin 1973). Consequently, it is not possible to determine whether the trapped sample is a statistically valid random sample.

As was discussed in Section 2.6.2, the behavioural responses of individuals when encountering a trap may differ depending on age, sex, individual experience of traps, the previous occupant of a trap, habitat features, climate and season. Abiotic factors such as trap spacing, trap position and the interval between trapping sessions have also been shown to influence trappability (Shillito 1963; Gurnell 1976; Stewart 1979; Gurnell and Gipps 1989). Further, live-trapping only shows where an individual was when it entered a trap. No inferences about where it was prior to capture can be made.

Only one trap was placed at each trap station in this study. This may have led to competition for traps in favoured habitats. However, the overall retrappability of individual *R. l. velutinus* was consistently high (see Figure 2.5) and it was a feature of the trapping program that residents not captured at a particular trap point were frequently caught in a nearby trap on the same day.

Recognition of these shortcomings is important, particularly if an extrapolation from trappable individuals to a whole population is made. At the level of the individual or local population however, live-trapping affords an opportunity to gather valuable information on the habits of small mammals provided such investigations are of sufficient length and intensity.

Ostfeld (1990) correctly pointed out that, in many scientific disciplines, the procedures employed to conduct an investigation often determine the questions that are asked. The trapping protocol in this study was designed primarily to clarify observations made by Stoddart and Challis (1991) about spacing behaviour in a local population of *R. l. velutinus*. Their observations were made from a relatively small (0.5ha) trapping grid during a much larger study of the sympatric native murid, *Pseudomys higginsi*. The observation that few male *R. l. velutinus* were trapped on their grid in winter in comparison to the summer breeding season (see Table 1.1) gave rise to several questions. Was there a sex bias in trappability? Did each sex

have different resource and habitat requirements? Or, was the presence of few males merely a product of the trapping regime? An extrapolation of their observations to a population level would be inappropriate without first showing that the observations were reproducible. For this reason, a more intensive investigation of a larger population of *R. l. velutinus* which aimed to provide answers to these questions was undertaken.

In the present study, individuals in the trappable population were equally likely to be trapped irrespective of sex, age, season or previous capture history. This was particularly evident during the winter trapping sessions when residents were caught repeatedly and there were few transient individuals (see Section 2.6.3). Further, it was shown that no apparent bias due to residual trap odours from previous occupants existed at this time.

Because each individual in the trappable population was equally re-trappable, the total number of captures, rather than the total number of individuals (which was low), could be used as an indicator of habitat preference. By comparing total captures in each of the habitat groups defined in Section 3.3, an indication of where males and females were most active was gained. No conclusions about residency in different habitat groups can be drawn from these data but they do provide an accurate assessment of where individuals of each sex are most likely to be captured.

Analysis of the trapping data provided answers to some of the questions posed at the beginning of this investigation. The bias towards fewer males in the trappable population observed by Stoddart and Challis (pers. comm.) during winter was also apparent in this study. It must be emphasized however, that no statistical significance is applied to these data. The 0.5ha grid maintained by Stoddart and Challis (1991) was located in an area of homogenous vegetation. The 4ha trapping grid used in this study encompassed heterogeneous vegetation types and resulted in the capture of proportionately more males. I predict that the use of an even larger, more diverse trapping grid would result in a sex ratio which approached parity.

6.3 Differential habitat use

Four habitat groups were defined using the classification and ordination procedures described in Section 3.2.2. These techniques

confirmed differences observed in the vegetation on the trapping grid. The habitat groups as they have been defined here relate to structurally and floristically distinct plant associations within a wet sclerophyll formation. Undoubtedly, transitional zones exist between these associations but the variation apparent in the vegetation had possibly been amplified by the effects of the 1967 wildfire (see Section 3.4).

Comparisons between capture rates revealed statistically significant differences between habitat groups and sexes both temporally and spatially. The most striking of these differences was apparent in the capture rates in habitat group 1a. A strong preference was shown by females for this habitat type throughout the study. This was most evident, however, during the winter trapping sessions when male captures were limited to the repetitive sampling (8 times) of only one surviving adult male. In comparison, three adult and two sub-adult females were captured 37 and 26 times respectively. The adults were also caught 12 times immediately adjacent (i.e., 1 trap away) to habitat group 1a, in habitat group 1b. One sub-adult was also caught three times in this same trap.

At the onset of breeding, the rate of captures for adult males in habitat group 1a increased seven-fold to exceed significantly the captures of adult females (13 males caught 57 times, 5 females caught 27 times: $c^2=10.01$, $P<0.01$).

Between-sex comparisons also differed in the other habitat groups but not to the same extent as habitat group 1a (see Table 4.2).

What was it about this habitat type that appeared attractive to females? Multiple regression analyses revealed that capture rates for each sex were directly related to the density of cover to one metre height (see Tables 4.7 and 4.8). This finding approximates to the results reported previously for forest populations of *R. l. velutinus* (Hocking 1975; Murray 1980; Driessen 1987) although the methodologies differed in each study. The area of the trapping grid with the most cover at this level was habitat group 1a (see Figure 4.4) where the fern, *Blechnum wattsii,* was ubiquitous. This may indicate that *R. l. velutinus* is a relative specialist in heterogeneous forest habitat. Few female and no male captures were recorded in habitat group 3 in 12 trapping sessions during winter and the breeding season. At the same time there

were few captures of *Pseudomys higginsi* and no captures of *Antechinus swainsonii*. It cannot be discounted that small sample sizes induced a trapping artefact but it is more likely that areas where ground cover is almost completely absent, such as group 3, are avoided. Lack of cover may lead to an increased susceptibility to avian, mammalian and reptilian predation or perhaps there is simply less food. *R. l. velutinus* is recorded as nocturnal in most habitats (Green 1967; Murray 1980) but in the present study, individuals were observed foraging at all times during the day in areas of dense cover. On several occasions, individuals released from one trap were re-released from another later during the same trap round. Areas of densest cover most likely afford maximum protection from aerial predation and an opportunity to forage for extended periods during daylight hours.

What is of particular interest is that the regression analyses showed that both sexes preferred areas of densest cover below one metre height, but such areas had female capture rates that far exceeded the rates for males. Why should females occupy areas of greatest cover? Parental investment in offspring by females is high and typically includes energetic costs and time constraints involved in gestation, lactation and rearing of young. Males, on the other hand, are often free of such constraints, particularly where an asynchronous mating system is apparent (Ims 1987). Therefore, the reproductive success of females is likely to be related to their ability to maintain resources and convert them into weaned offspring. Habitat use and social spacing in heterogeneous areas may thus be highly responsive to the distribution and abundance of resources such as cover and food availability (Ostfeld 1985; Ostfeld *et al.* 1985; Bergeron *et al.* 1990).

Price (1977) showed that in populations of heteromyid rodents, the frequency of capture of a species in a particular microhabitat could be directly related to foraging effort in that microhabitat. Similar correlations have been reported for *R. l. lutreolus* (Braithwaite and Gullan 1978; Braithwaite *et al.* 1978) and *R. l. velutinus* (Norton 1983, 1987) in lowland heath and buttongrass, *Gymnoschoenus sphaerocephalus,* communities.

No assessment of resource requirements was made in this study but the requirement for cover in forest populations of *R. l. velutinus* has been well

documented (Hocking 1975; Murray 1980). Driessen (1987) examined the dietary requirements of *R. l. velutinus* in wet sclerophyll forest using faecal analysis and concluded that it was cover rather than diet that played an important role in their selection of habitat.

There is no evidence to suggest that the areas where female capture rates are highest afford superior nutrition, protection from predation or other advantage. However, the persistence of high capture rates in both the breeding and non-breeding seasons suggests that these areas best fulfill the resource requirements of females. The marked increase in male capture rates in these areas after the onset of breeding suggests that their greatest resource requirement at that time might be females. This is consistent with predictions that it is mate receptivity, rather than habitat resources, that determines male fitness (Trivers 1972; Ims 1987, 1988).

Sexual differences in habitat use by rodents has been reported infrequently. Bowers and Smith (1979) found female deermice, *Peromyscus maniculatus,* occupying 'more favourable' microhabitats in xeric *Pinus ponderosa, Artemisia-Sarcobatus* and *Atriplex-Eurotia* communities in north western U. S. A.. Males were captured in the more xeric, 'less favourable' microhabitats. During their study, Bowers and Smith observed that most individuals remained in particular areas with females not showing any tendency to be caught near males (except during times of sexual activity). They concluded that differential sex distribution with females occupying areas of best resource maximized reproductive effort and survival of offspring by reducing predation on nest sites and lowering resource overlap. This selective advantage implied that there was intersexual competition since males were displaced to less favourable areas.

Morris (1984) disagreed. He tested the Bowers and Smith hypothesis with populations of white-footed mice, *P. leucopus* and meadow voles, *Microtus pennsylvanicus.* He also found sexual differences in habitat use by *P. leucopus* but offered an alternative hypothesis based on resource requirements. Put simply, females must choose safe nest sites and must spend considerable time near those sites during the rearing of young. Such sites were available mostly in the more mesic areas. Therefore, rather than reflecting an evolutionary strategy, differential habitat use merely reflected

reproductive constraints that limited females to areas with suitable nesting sites.

Seagle (1985) confirmed that forest populations of *P. leucopus* use microhabitat differentially, with females distributed in the areas of greatest cover. He suggested that the mechanism by which the sexes segregate was most likely intersexual aggression.

Belk *et al.* (1988) reported a trend for female *P. maniculatus, Zapus princeps, Clethrionomys gapperi* and *M. montanus* to occupy habitats with greater structural complexity in montane regions in Utah, U. S. A.. They agreed that areas of greatest cover reduced the risk of predation. They also postulated that in such areas, individuals (females) would be able to forage longer and more efficiently. They reasoned that because the costs of reproduction may be twice as great in females than in males (Stebbins 1977), any energetic advantage gained by being active in these areas must be adaptive. At the same time, males actually increase their reproductive fitness because of the benefits to actual or potential offspring gained by being raised in the areas of greatest cover.

Ostfeld *et al.* (1985) reported female-biased sex ratios, increased survivorship and higher rates of juvenile recruitment in California vole, *M. californicus,* communities occupying high-quality meadow habitat. They recorded a tendency for females to aggregate in the best areas and concluded that the manner in which females responded to spatial and temporal variation in resource quality reflected a reliance on resource acquisition to enhance reproductive success. They also found that female ranges tended to overlap during periods of sexual inactivity, indicating a lack of intrasexual interference. This was a common occurrence during the winter of the present study, where females active in habitat group 1a would often be captured in traps other females had occupied in the same trapping session (see Table 6.1). It was evident that each female was tolerant of the presence of others. This did not occur in the other habitat groups, where individuals, and particularly males, were more often caught in 'exclusive' traps.

It is interesting to speculate that, given that habitat group 1a best fulfills female resource requirements, then females which survive beyond one breeding season may remain in these areas. In this study, three adult

Table 6.1: Trap occupancy during the study. The number of trap entries for each session (=4 nights duration) is given after the trap session number.

TRAPPING SESSION	SEASON	TRAP OCCUPANCY (%)				
		1 FEMALE	1 MALE	>1F	>1M	MIXED
	Dispersal					
1 (n=29)		24.1	41.4	13.8	0.0	20.7
2 (n=28)		28.6	50.0	7.1	3.6	10.7
3 (n=26)		34.6	46.2	7.7	3.8	7.7
	Winter					
4 (n=21)		38.1	47.6	14.3	0.0	0.0
5 (n=23)		39.1	39.1	21.8	0.0	0.0
6 (n=25)		32.0	52.0	16.0	0.0	0.0
7 (n=24)		33.3	37.5	20.8	0.0	8.4
8 (n=26)		46.2	34.6	15.4	0.0	3.8
9 (n=31)		29.0	41.9	12.9	0.0	16.2
	Breeding					
10 (n=30)		13.3	50.0	6.7	6.7	23.3
11 (n=28)		17.9	42.9	0.0	7.1	32.1
12 (n=18)		16.7	33.3	0.0	11.1	38.9
13 (n=24)		29.2	54.2	0.0	0.0	16.7
14 (n=18)		38.9	38.9	0.0	0.0	22.2
15 (n=15)		53.4	20.0	0.0	13.3	13.3
	Dispersal					
16 (n=24)		29.2	29.2	12.5	8.3	20.8
17 (n=28)		28.6	46.4	10.7	0.0	14.3

Legend

1 Female - Number of traps which were only occupied by a single female in a single trapping session.

1 Male - Number of traps which were only occupied by a single male in a single trapping session.

> 1 F - Number of traps which were occupied by more than one female (but no males) per trapping session.

> 1 M - Number of traps which were occupied by more than one male (but no females) per trapping session.

Mixed - Number of traps which were occupied by males and females during one trapping session.

females born before 1989 were trapped repeatedly in group 1a along with two sub-adult females. The sub-adults may have been the offspring of one or more of the adults and an advantage may have been afforded these individuals.

Ranges measured using live-trapping on a grid bear no resemblance to actual spacing patterns but aggregation and neighbour tolerance have been reported for rodent species where non-breeding season resource requirements were not limiting (e.g., *P. leucopus,* Vestal and Hellack 1978; muskrats, *Ondatra zibethicus,* Caley and Boutin 1987).

Under what ecological conditions should such social spacing occur? Recently, research on social behaviour and space use has indicated that profound differences can occur in the degree of territoriality between sexes (e.g., Ostfeld *et al.* 1988). In an important review, Ostfeld (1990) emphasized that, in some rodents, males and females may interact with their environments in markedly different ways.

It appears that for the local population of *R. l. velutinus* under review, females occupy areas of best resource while males are relegated to peripheral habitat. During the non-breeding months, tolerance of female neighbours is evident and there is little intrasexual competition. Males occupy peripheral habitat at lower densities with little or no overlap in range (as defined by trap captures).

At the onset of breeding, females are concentrated in preferred habitat and it is to these areas that males are attracted. This is not inconsistent with the proposal that, at this time, females are territorial. There are fewer females caught during the breeding season and, after Session 10, none was captured in a trap previously occupied by another female (see Table 6.1). If females are territorial, there can be no monopoly of them by males defending territories. Instead, males should range widely and mate with receptive females. There is evidence that this was the case in the present study where numerous previously unmarked males entered the trappable population at the commencement of the breeding season, the majority of them being caught in habitat group 1a. Males which had overwintered in peripheral habitat on the trapping grid also moved into habitat group 1a.

Female *R. l. velutinus* are sexually receptive asynchronously and the

scenario described above supports Ostfeld's (1990) 'females in space and time' (FIST) hypothesis. This model predicts that for small mammals that opportunistically consume seeds, fruits, forbs and larvae, breeding females will be territorial and breeding males non-territorial.

In the light of this hypothesis, it is perhaps not surprising to find that the morpho-physiological indices defined in Section 5.1 did not indicate that individuals living in preferred habitat had a selective advantage over individuals in peripheral habitat. In wet sclerophyll forest, *R. l. velutinus* appears as a successful resident able to occupy most habitat types. Peripheral areas are occupied at lower densities than preferred habitat.

The most likely explanation for the low numbers of males in the trappable population recorded by Stoddart and Challis (unpubl. data) during winter is that their grid was situated entirely within a region of preferred habitat. Consequently, there was far greater activity by females with only occasional captures of males.

6.4 Future studies

One of the major findings of this study was the extent of repeated trapping of individual *R. l. velutinus*. As stated previously, there may have been individuals which never entered the trappable population, but individuals which were caught once were caught repeatedly. Such a readily trappable species may provide a model to test in greater detail several points raised in this thesis. Manipulation of a local population of *R. l. velutinus* by the selective removal or relocation of individuals, either temporarily or permanently, may shed light on the extent and seasonality of territory. It would be of considerable interest to determine how long an individual territory is maintained beforeits owner is usurped or it is incorporated into others.

An investigation which incorporated capture-mark-recapture techniques and radiotelemetry would determine the accuracy of *R. l. velutinus* territories defined by live-trapping. Radiotelemetry would also show whether females in preferred habitat share common resources such as burrows during non-breeding periods.

To test whether the differential use of habitat shown by the local

population studied here can be extrapolated to other populations in wet sclerophyll forests, a similar study in habitat undisturbed by wildfire could be conducted. If it is the case that sexual differences exist in the partitioning of habitat then there are implications for the management of this species following forestry practices. At present, the wildlife corridors that remain after coupes are logged are generally located along steep-sided gullies and creeks. Such areas are usually associated with dense stands of ferns such as *B. wattsii* and, if the findings of this study are substantiated, are most likely to be occupied by females. It may well be that areas of drier, more open forest need to be considered for reservation if this habitat is occupied by males during winter.

A study of resource requirements and utilization is also warranted. Procedures which investigate the seasonal energetic requirements of each sex, such as the use of radioactively-labelled water, oxygen and sodium, would be relatively straightforward given that individuals are so reliably re-trapped. Such a study should be combined with an investigation of the nutritive and calorific content of the foods consumed by *R. l. velutinus*. In this way, the preference for areas of dense cover to one metre height may be explained by dietary requirements, nesting requirements, cover or some combination of these factors.

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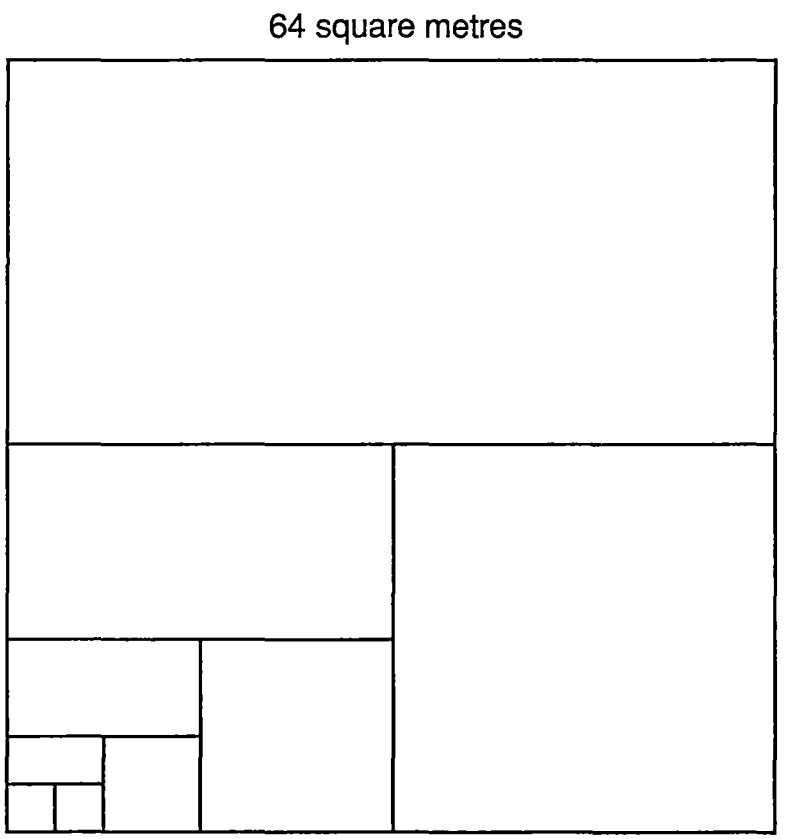
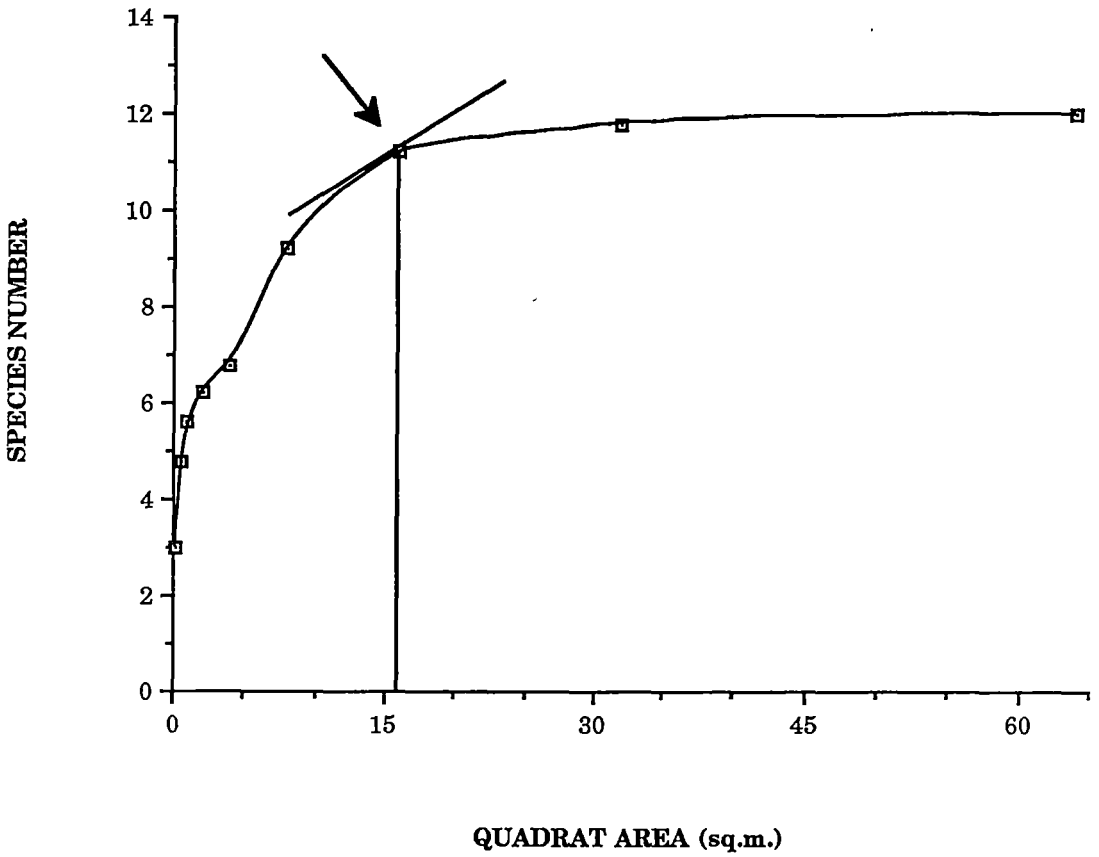
APPENDIX 1

THE DETERMINATION OF QUADRAT SIZE FOR VEGETATION ANALYSES

The quadrat size used for this study (16sq.m) was derived by the methodological minimal area technique (*sensu* Goldsmith and Harrison 1976). An initial 0.25sq. m quadrat was laid out and the number of vascular plant species was recorded. The sampling area was progressively doubled using a spiralling nested quadrat configuration until records of all species had been made up to a quadrat size of 64sq. m. This was repeated at five trap stations and an average relation curve was gained.

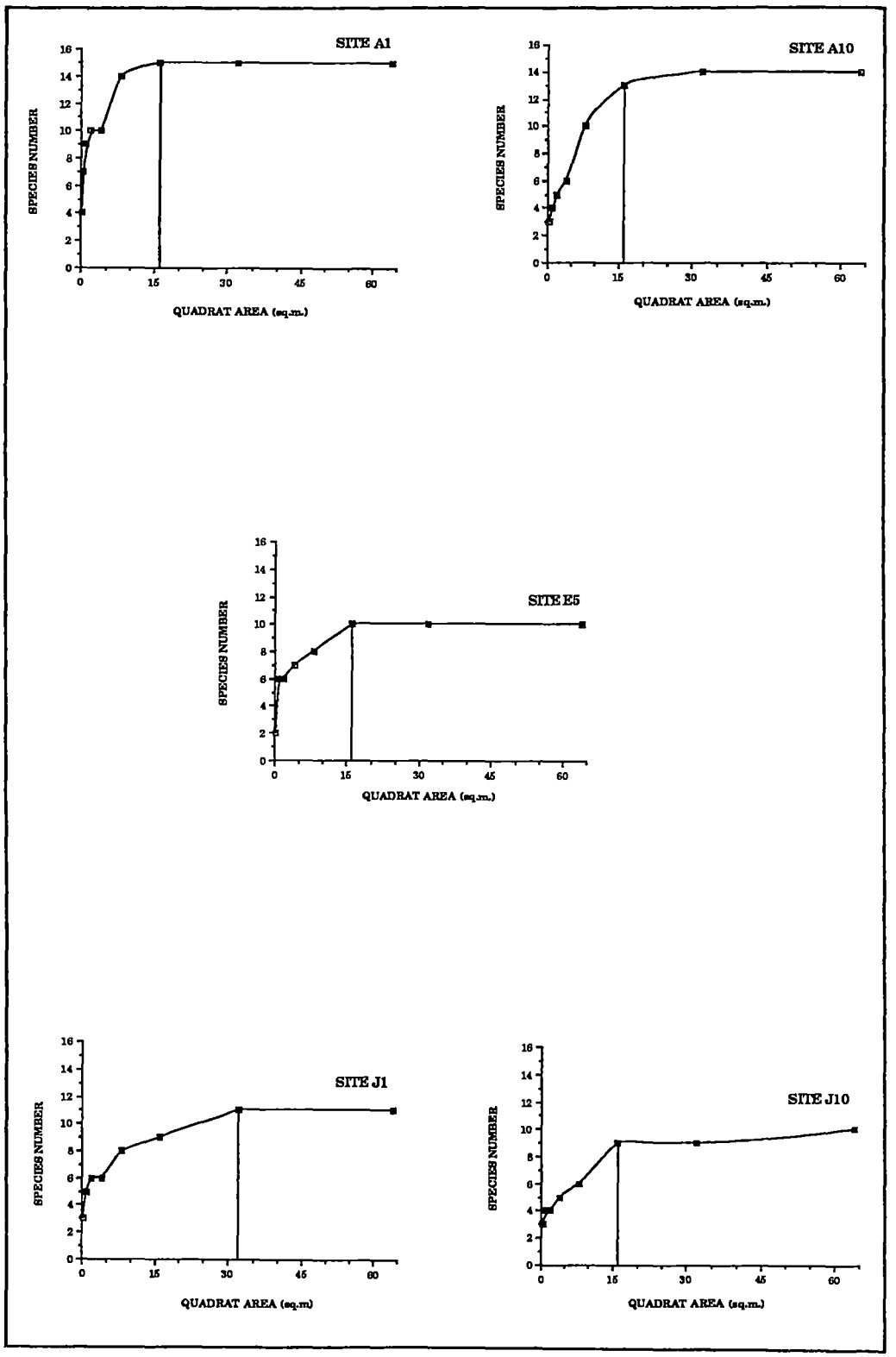


APPENDIX 1 cont.



Minimal area-species curve based on five quadrat samples.

APPENDIX 1 cont.



APPENDIX 2

VASCULAR PLANT SPECIES RECORDED ON THE TRAPPING GRID, SHOOBRIDGE BEND, MT. WELLINGTON, TASMANIA.

PTERIDOPHYTA

ASPIDACEAE

Polystichum proliferum (R.Br.) C.Presl.

BLECHNACEAE

Blechnum fluviatile (R.Br.) E.J.Löwe ex Salom
Blechnum penna-marina (Poir.) Kuhn
Blechnum wattsii Tind.

DAVALLIACEAE

Rumohra adiantiformis (Forst.f.) Ching

DENNSTAEDTIACEAE

Histiopteris incisa (Thunb.) J.Smith
Hypolepis rugosula (Labill.) J.Smith
Pteridium esculentum (Forst.f.) Cockayne

DICKSONIACEAE

Dicksonia antarctica Labill.

GRAMMITIDACEAE

Grammitis billardieri Willd.

LYCOPODIACEAE

Lycopodium varium R.Br.

POLYPODIACEAE

Microsorum diversifolium (Willd.) Copel.

MONOCOTYLEDONAE

CYPERACEAE

Carex appressa R.Br.
Gahnia grandis (Labill.) S.T.Blake
Uncinia tenella R.Br.

LILIACEAE

Astelia alpina R.Br.
Drymophila cyanocarpa R.Br.

ORCHIDACEAE

Caladenia gracilis R.Br.
Chiloglottis gunnii Lindley
Corybas sp.*
Pterostylis sp.*

POACEAE

Deyeuxia quadriseta (Labill.) Benth.
Deyeuxia rodwayi Vick.
Hierochloe redolens (Vahl) Roemer & Schultes
Holcus lanatus L.

*Because of their brief seasonal emergence, some members of Orchidaceae were difficult to identify to species level. On this basis, individual orchids could only be positively identified to species level when flowering; others were identified to genus level.

DICOTYLEDONAE

APIACEAE

Hydrocotyle hirta R.Br. ex A.Rich.

ASTERACEAE

Bedfordia salicina (Labill.) DC.
Cassinia aculeata (Labill.) R.Br.
Olearia argophylla (Labill.) Benth.
Olearia phlogopappa (Labill.) DC.
Olearia viscosa (Labill.) Benth.

CAROPHYLLACEAE

Stellaria flaccida Hook.

ELAEOCARPACEAE

Aristotelia peduncularis (Labill.) Hook.f.

EPACRIDACEAE

Cyathodes glauca Labill.
Cyathodes parvifolia R.Br.
Monotoca glauca (Labill.) Druce

ERICACEAE

Gaultheria hispida R.Br.

FABACEAE

Acacia dealbata Link
Acacia melanoxylon R.Br.

FAGACEAE

Nothofagus cunninghamii (Hook.) Oersted

GERANIACEAE

Geranium potentilloides L'Herit. ex DC.

HALORAGACEAE

Gonocarpus humilis Orch.
Gonocarpus teucrioides DC.

LAMIACEAE

Prostanthera lasianthos Labill.

MONIMIACEAE

Atherosperma moschatum Labill.

MYRTACEAE

Eucalyptus delegatensis R.Baker
Eucalyptus johnstonii Maiden
Eucalyptus obliqua L'Herit.
Eucalyptus regnans F.Muell.
Eucalyptus urnigera Hook.f.
Leptospermum lanigerum (Aiton) Smith

PITTOSPORACEAE

Billardiera longiflora Labill.
Pittosporum bicolor Hook.

PROTEACEAE

Hakea lissosperma R.Br.
Telopea truncata (Labill.) R.Br.

RANUNCULACEAE

Clematis aristata R.Br. ex DC.

RHAMNACEAE

Pomaderris apetala Labill.

ROSACEAE

Acaena novae-zelandiae Kirk

RUBIACEAE

Coprosma hirtella Labill.
Coprosma quadrifida (Labill.) Robinson

RUTACEAE

Correa lawrenciana Hook.
Phebalium squameum (Labill.) Engl.
Zieria arborescens Sims

THYMELAEACEAE

Pimelea cinerea R.Br.
Pimelea drupacea Labill.

URTICACEAE

Urtica incisa Poiret

WINTERACEAE

Tasmannia lanceolata (Poiret) A.C.Smith

APPENDIX 3

THE FREQUENCY OF OCCURRENCE OF VASCULAR PLANT SPECIES IN EACH HABITAT GROUP (%).

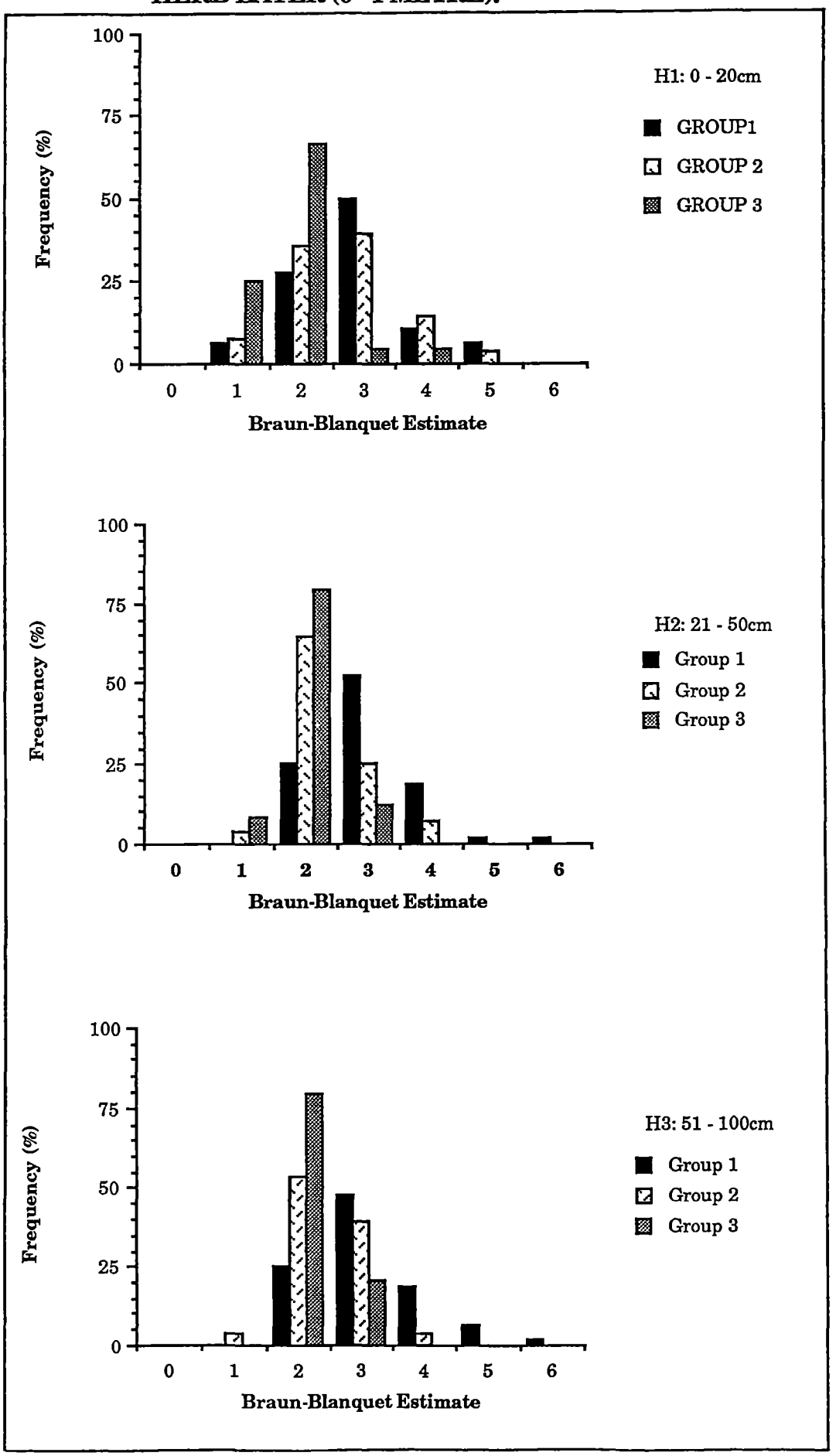
	HABITAT GROUP			
	1a	1b	2	3
Number of Quadrats	9	39	28	24
Dicotyledonae				
Acacia dealbata	33.3	12.8	46.4	75.0
Acacia melanoxylon	0.0	0.0	0.0	8.3
Acaena novae-zelandiae	0.0	7.7	0.0	0.0
Aristotelia peduncularis	0.0	20.5	32.1	12.5
Atherosperma moschatum	44.4	38.5	17.9	4.2
Bedfordia salicina	88.9	100.0	100.0	95.8
Billardiera longiflora	11.1	23.1	75.0	83.3
Clematis aristata	11.1	18.0	3.6	0.0
Coprosma hirtella	0.0	2.56	7.1	37.5
Coprosma quadrifida	0.0	0.0	0.0	4.2
Correa lawrenciana	0.0	7.7	28.6	8.3
Cyathodes glauca	11.1	7.7	35.7	25.0
Cyathodes parvifolia	0.0	0.0	7.1	0.0
Eucalyptus delegatensis	0.0	10.3	85.7	62.5
Eucalyptus johnstonii	0.0	0.0	0.0	8.3
Eucalyptus obliqua	0.0	5.1	0.0	45.8
Eucalyptus regnans	77.8	33.3	17.9	4.2
Eucalyptus urnigera	0.0	0.0	0.0	4.2
Gaultheria hispida	33.3	15.4	7.1	4.2
Geranium potentilloides	0.0	15.4	64.3	4.2
Gonocarpus humulus	0.0	0.0	0.0	4.2
Gonocarpus teucrioides	0.0	0.0	10.7	0.0
Hakea lissosperma	0.0	0.0	0.0	4.2
Hydrocotyle hirta	0.0	28.2	28.6	4.2
Leptospermum lanigerum	0.0	7.7	7.1	0.0
Monotoca glauca	11.1	2.6	7.1	12.5
Nothofagus cunninghamii	11.1	0.0	0.0	0.0
Olearia argophylla	88.9	94.9	60.7	83.3
Olearia phlogopappa	11.1	5.1	46.4	12.5
Olearia viscosa	0.0	12.8	39.3	20.8
Phebalium squameum	11.1	0.0	3.6	0.0
Pimelea cinerea	0.0	0.0	3.6	0.0
Pimelea drupacea	11.1	23.1	21.4	37.5
Pittosporum bicolor	77.8	41.0	28.6	50.0
Pomaderris apetala	88.9	100.0	100.0	95.8
Prostanthera lasianthos	0.0	23.1	14.3	58.3
Stellaria flaccida	0.0	0.0	3.6	0.0
Tasmannia lanceolata	66.7	23.1	3.6	8.3
Telopea truncata	0.0	0.0	3.6	0.0
Urtica incisa	11.1	18.0	0.0	0.0
Zieria arborescens	0.0	0.0	0.0	20.8

APPENDIX 3 cont.

	HABITAT GROUP			
	1a	1b	2	3
Number of Quadrats	9	39	28	24
Monocotyledonae				
Astelia alpina	0.0	2.6	0.0	0.0
Caledenia gracilis	0.0	0.0	3.6	0.0
Carex appressa	0.0	10.3	0.0	0.0
Chiloglottis gunnii	0.0	2.6	0.0	0.0
Corybas sp.	0.0	20.5	0.0	0.0
Deyeuxia quadriseta	0.0	7.7	0.0	0.0
Deyeuxia rodwayi	22.2	35.9	60.7	79.2
Drymophila cyanocarpa	33.3	46.2	53.6	66.7
Gahnia grandis	44.4	12.8	7.1	4.2
Hierochloe redolens	0.0	0.0	7.1	0.0
Holcus lanatus	0.0	2.6	35.7	8.3
Pterostylis sp.	0.0	2.6	7.1	8.3
Senecio linearifolius	0.0	10.3	46.4	0.0
Uncinia tenella	11.1	23.1	3.6	0.0
Pteridophyta				
Asplenium bulbiferum	22.2	64.1	21.4	0.0
Asplenium flabellifolium	0.0	0.0	0.0	4.2
Blechnum fluviatile	0.0	0.0	7.1	0.0
Blechnum penna-marina	0.0	2.6	0.0	0.0
Blechnum wattsii	88.9	74.4	3.6	37.5
Dicksonia antarctica	88.9	76.9	10.7	33.3
Grammitis billardierii	11.1	10.3	0.0	0.0
Histiopteris incisa	11.1	23.1	0.0	0.0
Hypolepis rugosula	33.3	10.3	0.0	0.0
Lycopodium varium	0.0	25.6	7.1	0.0
Microsorum diversifolium	33.3	64.1	89.3	29.2
Polystichum proliferum	88.9	97.4	78.6	62.5
Pteridium esculentum	11.1	0.0	0.0	4.2
Rumohra adiantiformis	33.3	15.4	14.3	0.0

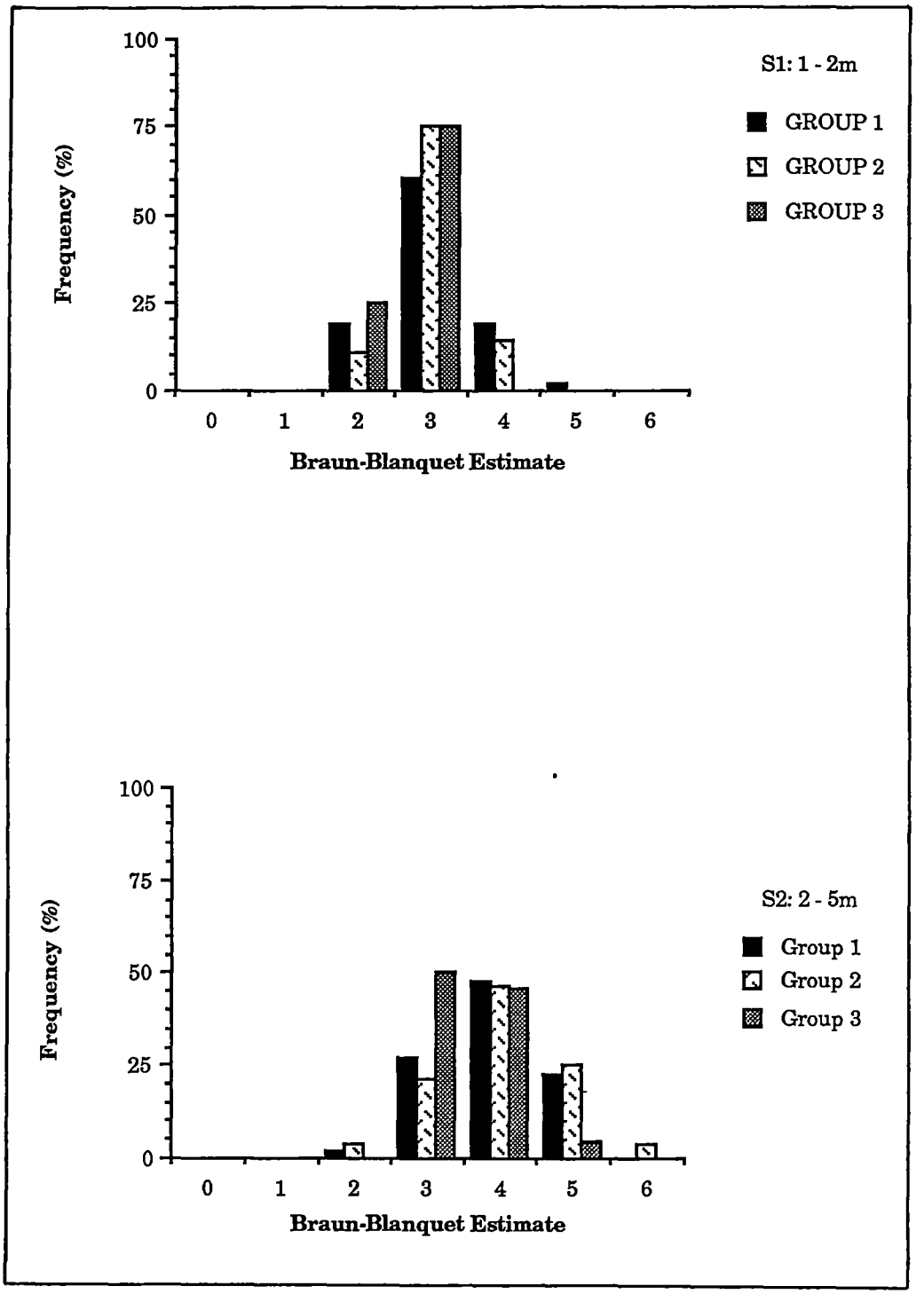
APPENDIX 4

THE FREQUENCY OF OCCURRENCE OF HABITAT ATTRIBUTES FOR EACH 'TWINSPAN' GROUP. HERB LAYER (0 - 1 METRE).



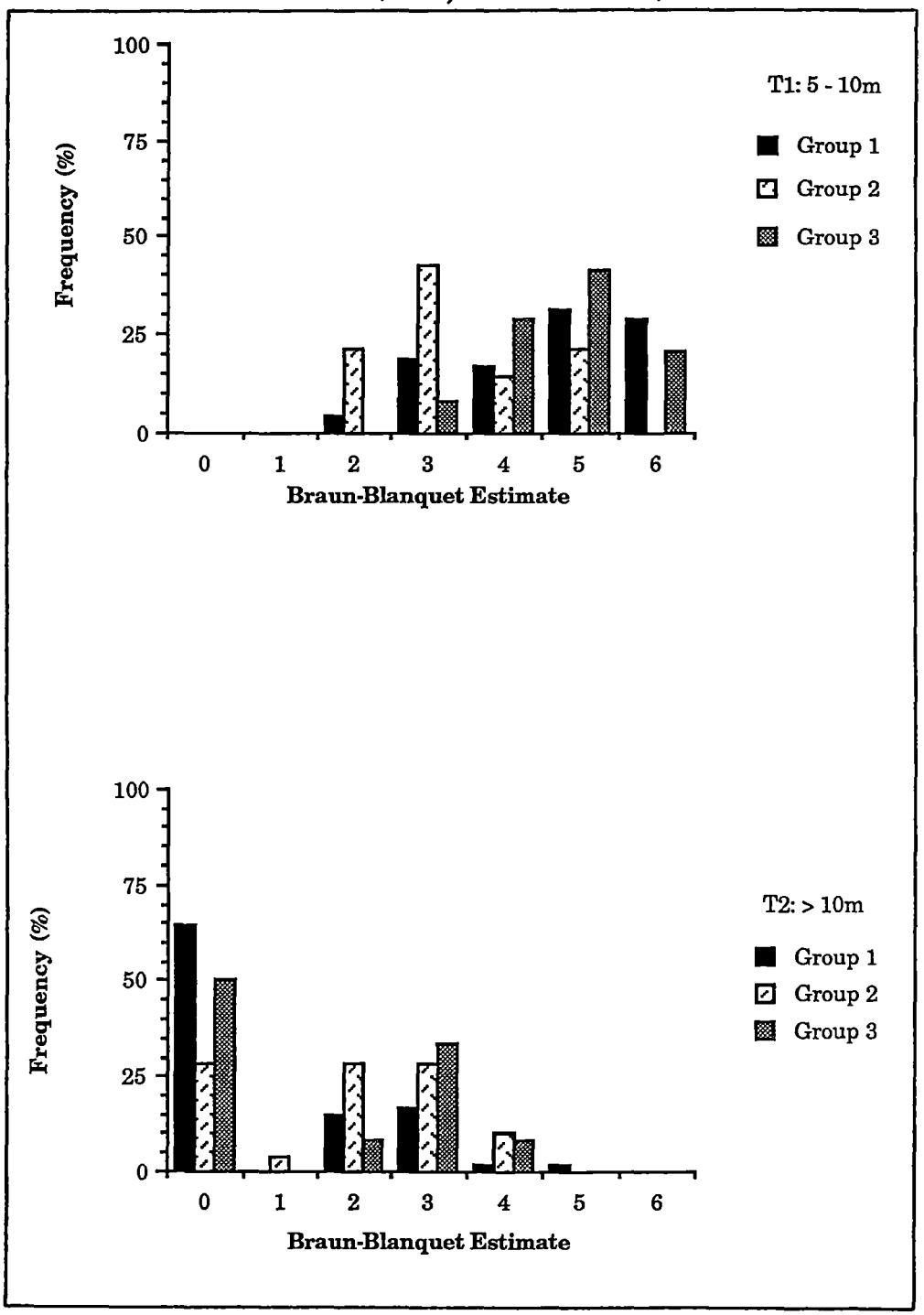
APPENDIX 4 cont.

THE FREQUENCY OF OCCURRENCE OF HABITAT ATTRIBUTES FOR EACH 'TWINSPAN' GROUP. SHRUB LAYER (1 - 5 METRES).



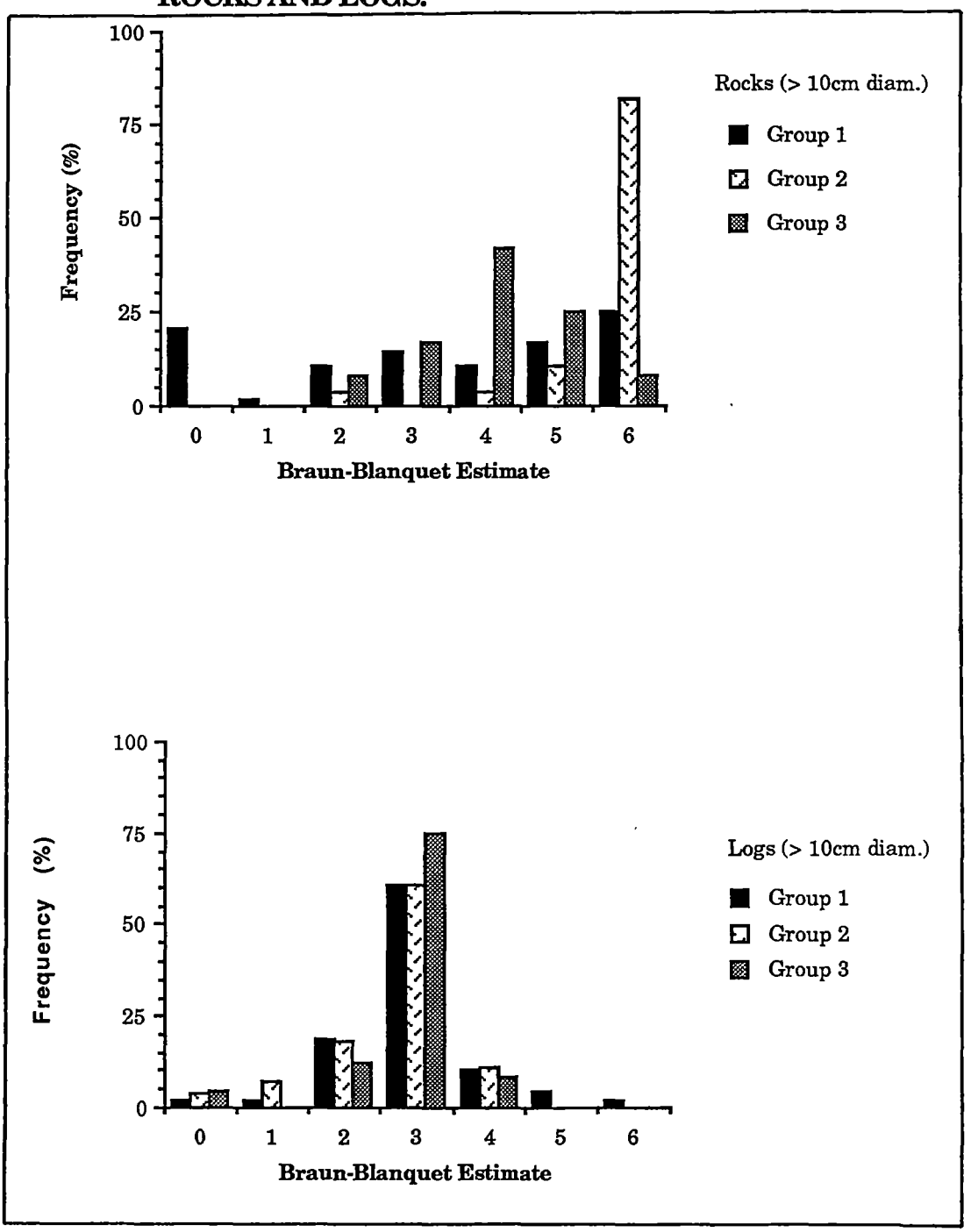
APPENDIX 4 cont.

THE FREQUENCY OF OCCURRENCE OF HABITAT ATTRIBUTES FOR EACH 'TWINSPAN' GROUP. TREE LAYER (5 -10; >10 METRES).



APPENDIX 4 cont.

THE FREQUENCY OF OCCURRENCE OF HABITAT ATTRIBUTES FOR EACH 'TWINSPAN' GROUP. ROCKS AND LOGS.



APPENDIX 5.1

1989 COHORT
TOTAL PLASMA PROTEINS AND ALBUMIN
(from Table 5.1)

TRAPPING SESSION	DATE	PROTEIN t	d.f	P	ALBUMIN t	d.f.	P
	Dispersal						
3	1.v.89	2.165	8	0.0623	2.585	8	0.0323
	Winter						
4	29.v.89	2.335	6	0.0582	0.046	6	0.9645
5	26.vi.89	1.040	6	0.3385	1.708	6	0.1385
6	24.vii.89	1.320	7	0.2282	3.896	7	0.0059**
7	21.viii.89	0.884	6	0.4109	0.742	6	0.4860
8	18.ix.89	1.672	7	0.1385	0.900	7	0.3979
9	16.x.89	0.836	10	0.4228	2.150	10	0.0571
	Breeding						
10	13.xi.89	0.073	17	0.9427	2.097	17	0.0513
11	11.xii.89	1.261	18	0.2234	0.364	18	0.7200
12	8.i.90	1.747	11	0.1084	0.277	11	0.7871
13	5.ii.90	0.777	9	0.4569	1.713	9	0.1250
14	5.iii.90	0.732	6	0.4920	0.458	6	0.6633
15	2.iv.90	n.a.*			n.a.		
	Dispersal						
16	30.iv.90	0.128	5	0.9032	0.166	5	0.8762
17	28.v.90	n.a.			n.a.		

* n.a.: not analysed - sample sizes too small. ** P<0.01 see text for discussion.

1989 COHORT
ERYTHROCYTE PARAMETERS
(from Tables 5.2a and 5.2b)

TRAPPING SESSION	DATE	HAEMATOCRIT			HAEMAGLOBIN CONCENTRATION			RED BLOOD CELL COUNT			MCHC			MCH			MCV		
		t	d.f	P	t	d.f.	P	t	d.f.	P	t	d.f.	P	t	d.f.	P	t	d.f.	P
	Dispersal																		
3	1.v.89	0.540	8	0.6040	1.254	8	0.2452	-	-	-	0.219	8	0.8322	-	-	-	-	-	-
	Winter																		
4	29.v.89	1.705	6	0.1392	1.74	6	0.1325	-	-	-	0.133	6	0.8983	-	-	-	-	-	-
5	26.vi.89	1.562	6	0.1693	0.414	6	0.6931	0.602	6	0.5690	0.503	6	0.6332	0.641	6	0.5451	0.527	6	0.6169
6	24.vii.89	0.793	7	0.4540	1.864	7	0.1046	1.013	7	0.3447	0.329	7	0.7516	0.549	7	0.6002	0.457	7	0.6612
7	21.viii.89	1.433	6	0.2018	1.626	6	0.1551	1.432	6	0.2020	0.170	6	0.8705	0.423	6	0.6872	0.563	6	0.5935
8	18.ix.89	0.204	7	0.8443	0.540	7	0.6060	0.036	7	0.9722	0.669	7	0.5249	0.265	7	0.5249	0.087	7	0.9331
9	16.x.89	1.053	13	0.3115	0.392	13	0.7014	0.355	13	0.7284	1.686	13	0.1156	0.116	13	0.9098	0.971	13	0.3491
	Breeding																		
10	13.xi.89	1.280	17	0.2178	2.381	17	0.0292	0.305	17	0.7638	3.062	17	0.0071**	0.417	17	0.6819	0.193	17	0.8439
11	11.xii.89	0.692	18	0.4976	1.315	18	0.2049	0.377	18	0.7108	2.319	18	0.0323	0.412	18	0.6855	0.58	18	0.5688
12	8.i.90	0.587	11	0.5692	0.247	11	0.8093	0.217	11	0.8323	0.558	11	0.5878	0.651	11	0.5283	0.966	11	0.3548
13	5.ii.90	1.864	9	0.0953	0.871	9	0.4064	0.837	9	0.4243	1.718	9	0.1199	0.444	9	0.6673	0.522	9	0.6143
14	5.iii.90	0.166	7	0.8729	0.067	7	0.9488	0.880	7	0.4083	0.427	7	0.6821	1.987	7	0.0873	1.529	7	0.1702
15	2.iv.90	n.a.			n.a.			n.a.			n.a.			n.a.			n.a.		
	Dispersal																		
16	30.iv.90	0.715	5	0.5067	0.730	5	0.4981	0.207	5	0.8443	0.335	5	0.7515	0.341	5	0.7466	0.513	5	0.6297
17	28.v.90	n.a.			n.a.			n.a.			n.a.			n.a.			n.a.		

* n.a.: not analysed - sample size too small.

** P<0.01 see text for discussion.

APPENDIX 5.3

LEUCOCYTES
1989 COHORT - MALES vs. FEMALES
(from Table 5.3)

TRAPPING SESSION	DATE	LEUCOCYTES t	d.f	P
	Dispersal			
3	1.v.89	1.814	8	0.1073
	Winter			
4	29.v.89	0.322	6	0.7511
5	26.vi.89	1.131	6	0.3012
6	24.vii.89	2.058	7	0.0786
7	21.viii.89	1.002	6	0.3552
8	18.ix.89	1.036	7	0.3306
9	16.x.89	1.458	10	0.1754
	Breeding			
10	13.xi.89	1.593	17	0.1295
11	11.xii.89	2.05	18	0.0553
12	8.i.90	2.731	11	0.0212
13	5.ii.90	0.695	9	0.5048
14	5.iii.90	0.217	7	0.8345
15	2.iv.90	n.a.*		
	Dispersal			
16	30.iv.90	0.344	5	0.7449
17	28.v.90	n.a.		

* n.a.: not analysed - sample sizes too small.

APPENDIX 5.4

1989 COHORT.
CORTICOSTERONE PARAMETERS.
(from Table 5.4)

TRAPPING SESSION	DATE	TOTAL CORTICOSTERONE			MCBC			FREE CORTICOSTERONE			CBG BOUND CORTICOSTERONE			ALBUMIN BOUND CORTICOSTERONE		
		t	d.f	P	t	d.f.	P	t	d.f.	P	t	d.f.	P	t	d.f.	P
	Dispersal															
3	1.v.89	0.239	6	0.8194	0.877	6	0.4144	1.258	6	0.2553	0.898	6	0.4039	1.906	6	0.1053
	Winter															
4	29.v.89	0.876	4	0.4370	0.547	4	0.6137	1.512	4	0.2052	0.301	4	0.7785	1.035	4	0.3589
5	26.vi.89	n.a.*			n.a			n.a			n.a			n.a		
6	24.vii.89	1.161	7	0 2837	0.875	7	0.4106	2.252	7	0.0590	0.935	7	0.3809	0.736	7	0.4855
7	21.viii.89	0.701	6	0.5095	0.528	6	0.6167	1.109	6	0.3101	0.563	6	0.5938	0.345	6	0.7416
8	18.ix.89	0 340	6	0.7451	0 441	6	0.6745	0.687	6	0.5176	0.451	6	0.6675	0.191	6	0.8545
9	16.x.89	1.695	10	0.1210	2.005	10	0.0728	1.638	10	0.1325	2.006	10	0.0726	0.772	10	0.4582
	Breeding															
10	13.xi.89	6.815	17	0.0001**	7.357	17	0.0001**	5.849	17	0.0001**	7.731	17	0.0001**	4.268	17	0.0005**
11	11.xii.89	10.409	18	0.0001**	12 628	18	0.0001**	5.467	18	0.0001**	12.470	18	0.0001**	6.878	18	0.0001**
12	8.i.90	7.170	11	0.0001**	8.298	11	0.0001**	4.977	11	0.0004**	8.243	11	0.0001**	3.619	11	0.0001**
13	5.ii.90	1.517	8	0.1679	2.116	8	0.0673	1.108	8	0.2999	2.103	8	0.0686	0.333	8	0.7478
14	5.iii.90	1.783	6	0.1249	2.136	6	0.0765	1.404	6	0.2098	2.121	6	0.0782	1.233	6	0.2637
15	2.iv.90	n.a			n.a			n.a			n.a			n.a		
	Dispersal															
16	30.iv.90	n.a.			n.a.			n.a.			n.a.			n.a.		
17	28.v.90	n.a			n.a			n.a			n.a			n.a		

* n.a.: not analysed - sample size too small.

** P<0.01 see text for discussion.

APPENDIX 5.5

HAEMATOLOGICAL PARAMETERS ETHER VALIDATION vs SESSION SIX (from Table 5.7)

BLOOD PARAMETER	VALIDATION FEMALES vs MALES (d.f.=13)	VALIDATION vs SESSION SIX FEMALES (d.f.=12)	MALES (d.f.=8)
HAEMATOCRIT (%)	t=1.619 P=0.129	t=2.949 P=0.012	t=0.994 P=0.349
PROTEIN ($g.dl^{-1}$)	t=0.137 P=0.893	t=0.685 P=0.506	t=1.365 P=0.209
HAEMOGLOBIN ($g.dl^{-1}$)	t=0.629 P=0.540	t=1.404 P=0.186	t=0.258 P=0.803
10^{-12} x RED CELL COUNT ($cells.L^{-1}$)	t=1.484 P=0.162	t=0.922 P=0.375	t=1.713 P=0.125
MCHC ($g.dl^{-1}$ red cells)	t=0.569 P=0.579	t=0.696 P=0.500	t=0.597 P=0.567
MCH (pg)	t=0.710 P=0.490	t=0.189 P=0.853	t=1.635 P=0.141
MCV (fL)	t=0.361 P=0.724	t=0.567 P=0.581	t=1.865 P=0.099
10-9 x LEUCOCYTE COUNT ($cells.L^{-1}$)	t=1.562 P=0.142	t=0.546 P=0.595	t=0.411 P=0.692
LYMPHOCYTES (%)	t=1.868 P=0.084	t=0.053 P=0.959	t=2.058 P=0.074
NEUTROPHILS (%)	t=1.843 P=0.088	t=0.042 P=0.967	t=2.058 P=0.074

APPENDIX 6

PREPARATION OF SOLUTIONS
(see Chapter 5).

HAYEM'S SOLUTION (for erythrocyte count).

Sodium Chloride	2.5g
Sodium Sulphate	6.25g
Mercuric Chloride	0.625g
Distilled Water	250ml

Dissolve Mercuric Chloride in warm water, add remainder and filter. Store at 4°C.

TURK'S SOLUTION (for leucocyte count).

Gentian Violet (1% aqueous)	1.0ml
Glacial Acetic Acid	1.0ml
Distilled Water	98.0ml

Store at 4°C.

WRIGHT'S BLOOD STAIN (for differential leucocyte counts).

Wright's Stain	0.3g
Absolute Methanol	100.0ml

DRABKIN'S SOLUTION (for haemoglobin concentration).

Sodium Bicarbonate	0.5g
Potassium Cyanide	25mg
Potassium Ferricyanide ($K_4Fe_3CN_6$)	100mg
Distilled Water	500ml

DEXTRAN-COATED CHARCOAL (for RIA method).

Activated charcoal (fines removed)	500mg
Dextran T70 (Pharmacia)	50mg
Phosphate buffer 0.05M pH7.4	400.0ml
Thimerosal	20mg

Add Dextran first, mix thoroughly, store at 4°C.

APPENDIX 7

Changes in the plasma proteins of adults born before 1989. (Values are means ± 1 SD, with the number of individuals in parentheses).

TRAPPING SESSION	DATE	PLASMA PROTEIN (g/dl)	PLASMA ALBUMIN (g/dl)
		FEMALES	
	Dispersal		
3	1.v.89	6.8±0.9 (3)	3.4±1.1 (3)
	Winter		
4	29.v.89	7.4±0.4 (3)	2.8±0.5 (3)
5	26.vi.89	7.4±0.7 (4)	3.6±0.7 (4)
6	24.vii.89	7.6±0.2 (4)	3.9±0.7 (4)
7	21.viii.89	7.7±0.4 (4)	3.9±0.7 (4)
8	18.ix.89	7.2±0.5 (3)	4.1±0.4 (3)
9	16.x.89	7.2 - 8.6 (2)	3.0 - 4.6 (2)
		MALES	
	Dispersal		
3	1.v.89	8.5 - 8.8	1.6 - 2.5
	Winter		
4	29.v.89	7.6	-
5	26.vi.89	7.6	3.3
6	24.vii.89	9.0	3.7
7	21.viii.89	8.2	3.8
8	18.ix.89	7.8	4.6
9	16.x.89	7.6	3.8

Changes in the plasma proteins of sub-adults born in 1990. (Values are means ± 1 SD, with the number of individuals in parentheses).

		FEMALES	
	Breeding		
14	5.iii.90	6.4±0.5 (3)	2.8±1.0 (3)
15	2.iv.90	7.2 - 7.8 (2)	4.4 - 4.6 (2)
	Dispersal		
16	30.iv.90	7.1±0.4 (4)	4.2±0.2 (4)
17	28.v.90	7.0±0.6 (5)	4.1±0.3 (5)
		MALES	
	Dispersal		
16	30.iv.90	6.0±0.8 (4)	3.6±0.6 (4)
17	28.v.90	6.0 - 6.8 (2)	4.74 (1)

Changes in the leucocyte indices of adults born before 1989 (Values are means ± 1 SD, with the number of individuals in parentheses).

TRAPPING SESSION	DATE	10-9 x LEUCOCYTE COUNT (cells.L-1)	NEUTROPHIL (%)	LYMPHOCYTE (%)
		FEMALES		
	Dispersal			
3	1.v.89	2.9±0.5 (3)	-	-
	Winter			
4	29.v.89	7.3±3.5 (3)	34.0±10.0 (3)	66.0±10.0 (3)
5	26.vi.89	4.9±2.4 (4)	14.0±7.4 (4)	86.0±7.4 (4)
6	24.vii.89	5.6±2.7 (4)	17.2±10.8 (4)	82.8±10.8 (4)
7	21.viii.89	6.4±0.8 (4)	7.0±5.8 (4)	93.0±5.8 (4)
8	18.ix.89	5.6±1.2 (3)	12.7±9.9 (3)	87.3±9.9 (3)
9	16.x.89	4.8 - 5.7	9.0 (2)	91.0 (2)
		MALES		
	Dispersal			
3	1.v.89	8.0	-	-
	Winter			
4	29.v.89	11.9	34	66
5	26.vi.89	17.8	10	90
6	24.vii.89	10.6	2	98
7	21.viii.89	12.1	19	81
8	18.ix.89	17.8	4	96
9	16.x.89	7.0	13	87

Changes in the leucocyte indices of sub-adults born in 1990 (Values are means ± 1 SD, with the number of individuals in parentheses).

		FEMALES		
	Breeding			
14	5.iii.90	12.3±1.6 (3)	18.3±1.2 (3)	81.7±1.2 (3)
15	2.iv.90	5.4 - 8.3	24 - 38	62 - 76
	Dispersal			
16	30.iv.90	15.2±9.6 (4)	12.7±5.8 (4)	87.3±5.8 (4)
17	28.v.90	12.5±4.9 (5)	15.2±6.0 (5)	84.8±6.0 (5)
		MALES		
	Dispersal			
16	30.iv.90	11.2±5.0 (4)	10.8±6.8 (4)	89.2±6.8 (4)
17	28.v.90	7.8 - 8.6 (2)	2 - 6 (2)	94 - 98 (2)

APPENDIX 7 cont.

Changes in the erythrocyte indices of adults born before 1989. (Values are means ± 1 SD, with number of individuals in parentheses).

TRAPPING SESSION	DATE	HAEMATOCRIT (%)	HAEMAGLOBIN ($g.dl^{-1}$)	10^{12}X RED BLOOD CELLS ($cells.L^{-1}$)	MCHC ($g.dl^{-1}$ red cells)	MCH (pg)	MCV (fl)
				MALES			
	Dispersal						
3	1.v.89	39.2 - 45.7 (2)	17.0 - 19.9 (2)	-	43.4 - 43.6 (2)	-	-
	Winter						
4	29.v.89	39.4	19.2	7.8	48.8	24.6	50.5
5	26.vi.89	39.9	16.7	4.5	41.8	37.2	89.0
6	24.vii.89	35.2	14.2	7.0	41.6	20.3	50.3
7	21.viii.89	41.8	16.6	7.7	39.8	21.6	54.4
8	18.ix.89	40.1	15.4	6.8	38.4	22.8	59.4
9	16.x.89	45.9	17.2	7.2			
				FEMALES			
	Dispersal						
3	1.v.89	41.6±2.7 (3)	17.2±0.4 (3)	-	41.4±2.2 (3)	-	-
	Winter						
4	29.v.89	46.4±2.5 (3)	15.8±1.2 (3)	-	33.9±1.0 (3)	-	-
5	26.vi.89	45.2±2.8 (4)	17.9±1.9 (4)	7.7±0.9 (4)	37.8±2.0 (4)	22.4±1.1 (4)	59.4±4.3 (4)
6	24.vii.89	43.0±2.7 (4)	17.4±0.8 (4)	7.6±0.9 (4)	40.5±1.4 (4)	23.1±1.4 (4)	49.9±18.3 (4)
7	21.viii.89	42.3±2.1 (4)	17.5±1.5 (4)	8.0±1.0 (4)	41.2±1.6 (4)	22.0±1.0 (4)	53.6±4.3 (4)
8	18.ix.89	43.3±3.2 (3)	17.2±0.9 (3)	7.6±1.3 (3)	39.8±1.4 (3)	22.3±2.4 (3)	56.0±5.3 (3)
9	16.x.89	44.0 - 44.2 (2)	16.8 - 18.2 (2)	6.6 - 7.4 (2)	38.1 - 41.3 (2)	22.6 - 27.3 (2)	59 3 - 66.1 (2)

Changes in the erythrocyte indices of young born in 1990. (Values are means ± 1 SD, with number of individuals in parentheses).

				FEMALES OF 1990			
	Breeding						
14	5.iii.90	47.6±3.0 (3)	17.4±1.3 (3)	9.1±1.2 (3)	36.5±0.6 (3)	19.3±1.2 (3)	52.8±3.8 (3)
15	2.iv.90	45.0 - 47.8 (2)	16.7 - 17.5 (2)	6.8 - 7.5 (2)	36.7 - 37.0 (2)	23.9 - 24.5 (2)	63.8 - 66.2 (2)
	Dispersal						
16	30.iv.90	46.4±3.2 (3)	16.5±2.0 (3)	6.7±0.3 (3)	35.6±0.3 (3)	24.7±3.4 (3)	69.3±4.8 (3)
17	28.v.90	46.6±5.2 (4)	17.3±1.0 (4)	7.0±1.0 (4)	37.2±2.1 (4)	24.9±1.3 (4)	66.9±3.2 (4)
				MALES OF 1990			
	Dispersal						
16	30.iv.90	47.7±1.6(4)	18.2±0.6 (4)	6.9±0.7 (4)	38.1±2.3 (4)	26.4±2.9 (4)	69.5±8.7 (4)
17	28.v.90	41.2 - 49.1 (2)	14.0 - 14.9 (2)	5.4 - 6.0 (2)	28.5 - 36.2 (2)	24.6 - 25.9 (2)	68.0 - 90.9 (2)

APPENDIX 7 cont.

Changes in the steroid indices of adults born before 1989
(Values are means ± 1 SD, with number of individuals in parentheses).

TRAPPING SESSION	DATE	TOTAL CORTICOSTERONE (μM)	MCBC (μM)	FREE CORTICOSTERONE (μM)	CBG BOUND (μM)	ALBUMIN BOUND (μM)
				MALES		
	Dispersal					
3	1.v.89	5.8 (1)	5.8 (1)	0 3 (1)	5.1 (1)	0.4 (1)
	Winter					
4	29.v.89	-	-	-	-	-
5	26.vi.89	2.4 (1)	1.9 (1)	0.2 (1)	1.6 (1)	0.6 (1)
6	24.vii.89	4.6 (1)	3.2 (1)	0.4 (1)	2.9 (1)	1.3 (1)
7	21.viii.89	3.2 (1)	2.3 (1)	0.3 (1)	2.0 (1)	0.9 (1)
8	18.ix.89	2.3 (1)	1.7 (1)	0.2 (1)	1.4 (1)	0.7 (1)
9	16.x.89	2.5 (1)	2.0 (1)	0.2 (1)	1.7 (1)	0.6 (1)
				FEMALES		
	Dispersal					
3	1.v.89	9.2±0.8 (3)	6.6±2.6 (3)	0.9±0.6 (3)	6.1±2.0 (3)	2.1±1.4 (3)
	Winter					
4	29.v.89	6.8±2.6 (3)	4.1±1.1 (3)	0.8±0.4 (3)	3.9±1.1 (3)	2.0±1.2 (3)
5	26.vi.89	5.1±1.4 (4)	4 2±3.0 (4)	0.4±0.2 (4)	3.6±2.1 (4)	1.2±0.7 (4)
6	24.vii.89	6.0±1.7 (4)	3.5±1.1 (4)	0 6±0.2 (4)	3.3±1.1 (4)	2.1±0 5 (4)
7	21.viii.89	6.5±1.4 (4)	3.8±0.4 (4)	0.6±0 2 (4)	3.7±0.4 (4)	2.2±0.8 (4)
8	18.ix.89	7.0±1.0 (3)	4.0±0.8 (3)	0.7±0.1 (3)	3.9±0.8 (3)	2.4±0.3 (3)
9	16.x.89	8.8 - 8.9 (2)	4.9 - 5.1 (2)	0.8 - 1.2 (2)	4.7 - 4.9 (2)	3.0 - 3.1 (2)

Changes in the steroid indices of sub-adults born in 1990
(Values are means ± 1 SD, with number of individuals in parentheses).

				FEMALES OF 1990		
	Breeding					
14	5.iii.90	9.7±2.7 (3)	5.3±2.4 (3)	1.C±0.1 (3)	5.1±2.3 (3)	3.5±0.4 (3)
15	2.iv.90	7.7 - 14.7 (2)	4.8 - 8.4 (2)	0.6 - 1.4 (2)	4.6 - 8.2 (2)	2.5 - 5.1 (2)
	Dispersal					
16	30.iv.90	7.7±1.7 (3)	4.4±1.4 (3)	0 6±0.1 (3)	4.3±1.4 (3)	2.7±0.4 (3)
17	28.v.90	7.3±0.8 (4)	4.3±0.4 (4)	0.7±0.1 (4)	4.1±0.4 (4)	2.5±0.4 (4)
				MALES OF 1990		
	Dispersal					
16	30.iv.90	8.0±1.6 (4)	5.1±1.1 (4)	0.6±0.2 (4)	4.9±1.1 (4)	2.3±0.5 (4)
17	28.v.90	6.8 (1)	3.7 (1)	0.6 (1)	3.5 (1)	2.6 (1)

APPENDIX 8

ADULT FEMALES AND MALES BORN BEFORE 1989 vs. FEMALES AND MALES BORN IN 1989
TOTAL PLASMA PROTEINS AND ALBUMIN

TRAPPING SESSION	DATE	PROTEIN t	d.f	P	ALBUMIN t	d.f.	P
		FEMALES					
	Dispersal						
3	1.v.89	0.881	5	0.4188	0.791	5	0.4647
	Winter						
4	29.v.89	2.366	5	0.0643	0.602	5	0.5735
5	26.vi.89	1.721	7	0.1289	1.046	7	0.3302
6	24.vii.89	2.422	7	0.0459	1.739	7	0.1256
7	21.viii.89	2.432	7	0.0453	0.134	7	0.8973
8	18.ix.89	0.581	7	0.5797	0.225	7	0.8283
9	16.x.89	1.715	7	0.1301	0.335	7	0.7331
		MALES					
	Dispersal						
3	1.v.89	n.a*.			n.a.		
	Winter						
4	29.v.89	n.a.			n.a.		
5	26.vi.89	n.a.			n.a.		
6	24.vii.89	n.a.			n.a.		
7	21.viii.89	n.a.			n.a.		
8	18.ix.89	n.a.			n.a.		
9	16.x.89	n.a.			n.a.		

ADULT FEMALES AND MALES BORN IN 1989 vs. FEMALES AND MALES BORN IN 1990
TOTAL PLASMA PROTEINS AND ALBUMIN

TRAPPING SESSION	DATE	PROTEIN t	d.f	P	ALBUMIN t	d.f.	P
		FEMALES					
	Breeding						
14	5.iii.90	0.718	4	0.5127	1.967	4	0.1206
15	2.iv.90	n.a.*			n.a.		
	Dispersal						
16	30.iv.90	0.417	6	0.6940	1.321	6	0.2571
17	28.v.90	n.a.			n.a.		
		MALES					
	Dispersal						
16	30.iv.90	6.621	5	0.0012**	0.567	5	0.5950
17	28.v.90	n.a.			n.a.		

*n.a.: not analysed - sample sizes too small.
** P<0.01 see text for discussion.

APPENDIX 8 cont.

LEUCOCYTES

ADULT FEMALES AND MALES BORN BEFORE 1989 vs. FEMALES AND MALES BORN IN 1989

TRAPPING SESSION	DATE	LEUCOCYTES t	d.f	P
		FEMALES		
	Dispersal			
3	1.v.89	2.386	5	0.0627
	Winter			
4	29.v.89	0.572	5	0.5922
5	26.vi.89	0.902	7	0.3970
6	24.vii.89	1.232	7	0.2577
7	21.viii.89	0.226	7	0.8273
8	18.ix.89	1.899	7	0.0994
9	16.x.89	n.a.		
		MALES		
	Dispersal			
3	1.v.89	n.a.		
	Winter			
4	29.v.89	n.a.		
5	26.vi.89	n.a.		
6	24.vii.89	n.a.		
7	21.viii.89	n.a.		
8	18.ix.89	n.a.		
9	16.x.89	n.a.		

LEUCOCYTES

ADULT FEMALES AND MALES BORN IN 1989 vs. FEMALES AND MALES BORN IN 1990

		FEMALES		
	Breeding			
14	5.iii.90	0.049	5	0.9628
15	2.iv.90	n.a.		
	Dispersal			
16	30.iv.90	0.834	5	0.4424
17	28.v.90	1.176	4	0.3048
		MALES		
	Dispersal			
16	30.iv.90	2.122	5	0.0873
17	28.v.90	n.a.		

* n.a.: not analysed - sample sizes too small.

APPENDIX 8 cont.

ADULT FEMALES AND MALES BORN BEFORE 1989 vs. FEMALES AND MALES BORN IN 1989

ERYTHROCYTE PARAMETERS.

TRAPPING SESSION	DATE	HAEMATOCRIT			HAEMAGLOBIN CONCENTRATION			RED BLOOD CELL COUNT			MCHC			MCH			MCV		
		t	d.f	P	t	d.f.	P	t	d.f.	P	t	d.f.	P	t	d.f.	P	t	d.f.	P
								FEMALES											
	Dispersal																		
3	1.v.89	0.097	5	0.9267	1.238	5	0.2707	0.333	5	0.7525	0.515	5	0.6284	0.544	5	0.6098	0.432	5	0.6835
	Winter																		
4	29.v.89	0.633	5	0.5543	1.274	5	0.2586	1.485	5	0.1978	1.125	5	0.3116	0.587	5	0.5824	0.853	5	0.4327
5	26.vi.89	0.499	7	0.6328	1.363	7	0.2151	1.287	7	0.2391	1.558	7	0.1631	1.671	7	0.1386	1.500	7	0.1773
6	24.vii.89	3.712	7	0.0075**	4.499	7	0.0028**	0.540	7	0.6058	1.670	7	0.1388	1.572	7	0.1600	1.688	7	0.1354
7	21.viii.89	0.963	7	0.3676	0.058	7	0.9554	1.624	7	0.1484	2.291	7	0.0557	2.101	7	0.0738	2.360	7	0.0503
8	18.ix.89	1.198	7	0.2700	0.591	7	0.5728	0.013	7	0.9902	1.580	7	0.1581	0.4730	7	0.6506	0.810	7	0.4420
9	16.x.89	1.018	7	0.3426	0.121	7	0.9070	0.032	7	0.9752	2.756	7	0.0282	0.218	7	0.8337	1.618	7	0.1496
								MALES											
	Dispersal																		
3	1.v.89	0.685	6	0.5192	0.477	6	0.6505	0.872	6	0.4166	0.126	6	0.9037	0.499	6	0.6354	0.523	6	0.6200
	Winter																		
4	29.v.89	n.a.*			n.a.			-	-	-	n.a.			-	-	-	-	-	-
5	26.vi.89	n.a.			n.a.			n.a.			n.a.			n.a.			n.a.		
6	24.vii.89	n.a.			n.a.			n.a.			n.a.			n.a.			n.a.		
7	21.viii.89	n.a.			n.a.			n.a.			n.a.			n.a.			n.a.		
8	18.ix.89	n.a.			n.a.			n.a.			n.a.			n.a.			n.a.		
9	16.x.89	n.a.			n.a.			n.a.			n.a.			n.a.			n.a.		

* n.a.: not analysed - sample size too small.

** P<0.01 see text for discussion.

APPENDIX 8 cont.

FEMALES AND MALES BORN IN 1989 vs. FEMALES AND MALES BORN IN 1990
ERYTHROCYTE PARAMETERS

TRAPPING SESSION	DATE	HAEMATOCRIT			HAEMAGLOBIN CONCENTRATION			RED BLOOD CELL COUNT			MCHC			MCH			MCV		
		t	d.f	P	t	d.f.	P	t	d.f.	P	t	d.f.	P	t	d.f.	P	t	d.f.	P
								FEMALES											
	Breeding																		
14	5.iii.90	2.129	5	0.0865	1.727	5	0.1447	2.316	5	0.0684	0.297	5	0.7782	1.510	5	0.1915	0.731	5	0.4977
15	2.iv.90	n.a.			n.a.			n.a.			n.a.			n.a.			n.a.		
	Dispersal																		
16	30.iv.90	0.146	5	0.8895	0.262	5	0.8041	0.130	5	0.9013	0.064	5	0.9513	0.278	5	0.7923	0.150	5	0.8869
17	28.v.90	0.509	4	0.6378	0.824	4	0.4561	0.115	4	0.9137	0.648	4	0.5526	1.291	4	0.2663	0.777 4	4	0.4803
								MALES											
	Dispersal																		
16	30.iv.90	1.514	5	0.1904	4.112	5	0.0092*	0.553	5	0.6039	1.379	5	0.2264	1.449	5	0.2071	0.556	5	0.6024
17	28.v.90	n.a.			n.a.			n.a.			n.a.			n.a.			n.a.		

* n.a.: not analysed - sample size too small.

** P<0.01 see text for discussion.

APPENDIX 8 cont.

ADULT FEMALES AND MALES BORN BEFORE 1989 vs. FEMALES AND MALES BORN IN 1989
CORTICOSTERONE PARAMETERS

TRAPPING SESSION	DATE	TOTAL CORTICOSTERONE			MCBC			FREE CORTICOSTERONE			CBG BOUND CORTICOSTERONE			ALBUMIN BOUND CORTICOSTERONE		
		t	d.f	P	t	d.f.	P	t	d.f.	P	t	d.f.	P	t	d.f.	P
								FEMALES								
	Dispersal															
3	1.v.89	0.482	4	0.6547	0.347	4	0.7464	0.993	4	0.3770	0.192	4	0.8569	0.398	4	0.7111
	Winter															
4	29.v.89	0.875	4	0.4309	1.215	4	0.2911	0.298	4	0.7803	1.207	4	0.2940	0.005	4	0.9965
5	26.vi.89	1.503.	6	0.1835	0.538	6	0.6101	1.151	6	0.2936	0.867	6	0.4190	1.270	6	0.2511
6	24.vii.89	1.256	7	0.2493	0.668	7	0.5258	2.279	7	0.0567	0.725	7	0.4922	1.585	7	0.1569
7	21.viii.89	1.115	7	0.3018	1.262	7	0.2473	0.808	7	0.4457	1.261	7	0 2477	0.456	7	0.6624
8	18.ix.89	0.267	6	0.7985	0.170	6	0.8705	0.611	6	0.5633	0.186	6	0.8585	0.224	6	0.8304
9	16.x.89	n.a.			n.a.			n.a.			n.a.			n.a.		
								MALES								
	Dispersal															
3	1.v.89	n.a.			n.a.			n.a.			n.a.			n.a.		
	Winter															
4	29.v.89	n.a.			n.a.			n.a.			n.a.			n.a.		
5	26.vi.89	n.a			n.a.			n.a.			n.a.			n.a.		
6	24.vii.89	n.a.			n.a.			n.a.			n.a.			n.a.		
7	21.viii.89	n.a.			n.a.			n.a.			n.a.			n.a.		
8	18.ix.89	n.a.			n.a.			n.a.			n.a.			n.a.		
9	16.x.89	n.a.			n.a.			n.a.			n.a.			n.a.		

FEMALES AND MALES BORN IN 1989 vs. FEMALES AND MALES BORN IN 1990
CORTICOSTERONE PARAMETERS

		t	d.f	P	t	d.f.	P	t	d.f.	P	t	d.f.	P	t	d.f.	P
								FEMALES								
	Breeding															
14	5.iii.90	0.551	4	0.6107	0.687	4	0.5296	0.972	4	0.3862	0.697	4	0.5241	0.020	4	0.9850
15	2.iv.90	n.a.			n.a.			n.a.			n.a.			n.a.		
	Dispersal															
16	30.iv.90	n.a.			n.a.			n.a.			n.a.			n.a.		
17	28.v.90	n.a.			n.a.			n.a.			n.a.			n.a.		
								MALES								
	Dispersal															
16	30.iv.90	0.394	5	0.7096	0 575	5	0.5901	1.765	5	0.1377	0.496	5	0.6413	1.753	5	0.1401
17	28.v.90	n.a.			n.a.			n.a.			n.a.			n.a.		

* n a.: not analysed - sample size too small.